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BENTHISCH-PELAGISCHE KOPPLUNG AUS BENTHISCHER SICHT

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Zusammenfassung

Eine Lebensgrundlage der Organismen, die unterhalb der belichteten Zone des Meeres am Meeresboden, im Benthal, leben, ist die pflanzliche Produktion im Wasser, dem Pelagial. Der quantitative Zusammenhang zwischen pelagisch produziertem Material und der Aktivität der Organismen im Meeresboden wurde 1973 von Hargrave durch ein Modell beschrieben. Obwohl dieses Modell aus 20 Daten von anders-artigen Meeresgebieten abgeleitet wurde, scheint es auch auf die Kieler Bucht zuzutreffen. Etwa 1/3 der im Wasser produzierten pflanzlichen Substanzen verbleibt den Organismen am Meeresboden als Nahrung, wenn man 1 m^2 Meeresboden mit dem unmittelbar darüber liegendem Wasser vergleicht.

Ziel der vorliegenden Arbeit ist, dieses Modell einer Kopplung zwischen den beiden Lebensräumen Benthal und Pelagial realistisch zu erweitern. Es wird berücksichtigt, daß 1) der Partikelfluß aus dem Pelagial ins Benthal eine laterale, horizontale Komponente hat, daß 2) Bodentiere aktiv Nahrung aus dem Wasser herausfangen, daß 3) die Tiere im Sediment durch ihre mechanische Aktivität (Bioturbation) Partikel vergraben oder zurück ins Wasser geben sowie Wasser durchs Sediment pumpen, und daß schließlich 4), physikalische Prozesse wie Erosion und Diffusion eine Rolle spielen.

Da viele der beteiligten Prozesse saisonal gesteuert sind, ist zu verschiedenen Jahreszeiten eine unterschiedliche Kopplung der beiden Lebensräume zu erwarten. Die aufgeführten Transportprozesse haben zur Folge, daß Menge und Qualität des organischen Materials im Sediment, also die Nahrung der Bodentiere, sich ebenfalls saisonal verändert. Die Körpermasse der Bodentiere selbst stellt nur einen geringen Anteil an dem gesamten organischen Material im Meeresboden.

Wenn neu produziertes Algenmaterial zum Meeresboden absinkt, ein Ereignis, das besonders im Frühjahr und Herbst von Bedeutung ist, reagieren die Bodentiere ohne Zeitverzögerung. Dieser Befund läßt sich für die Kieler Bucht, die zentrale Ostsee und auch für das Europäische Nordmeer bestätigen. In der Kieler Bucht erhöhen die Organismen innerhalb einer Woche ihren Stoffumsatz dabei um den Faktor 7. Der Effekt der Nahrungszufuhr übertrifft den Effekt von Temperaturänderungen im Laufe eines Jahres eindeutig.
Kleine Organismen profitieren unmittelbar von solchen Eintragsereignissen. Bakterien verbrauchen etwa 60-80%, Einzeller 20% der eingetragenen Nahrung. Für mehrzellige Organismen verbleibt nur wenig, sie können aber als zweites Glied der Nahrungskette auch die neu produzierten Bakterien und Einzeller nutzen. Besonders im Frühjahr füllen Tiere wie die Muschel *Macoma baltica* ihren Vorrat an Reservestoffen auf, ohne den sie später im Sommer nicht zur Reproduktion fähig wären. Die beiden wichtigsten Eintragsereignisse im Frühjahr und Herbst wirken als Zeitgeber für die Fortpflanzungszyklen. Auch durch Verhaltensweise wird die Nutzung der frisch eingetragenen Nahrung verbessert. In der Norwegischen Tiefsee wurde beobachtet, daß Spritzwürmer Nahrung von der Oberfläche des Meeresbodens in tiefe Gangsysteme ziehen und damit der Konkurrenz der Oberflächenbewohner entgehen.
Während des Frühjahres und des Herbstes kommen jeweils innerhalb weniger Tage etwa 2/3 der Gesamtmenge an Nahrung aus dem Wasser am Meeresboden an. Der Meeresboden ist nach solchen Ereignissen grün von einzelligen Algen. Im Winter und vereinzelt auch nach Sommerstürmen werden außerdem noch Großalgen, insbesondere Rotalgen, in den Flachwassergebieten abgerissen, zerrieben und in größere Tiefen verfrachtet. Die Nahrungsversorgung ist ungleichmäßig. Auf kurze Überflußphasen folgen längere Hungerphasen. Das hat wichtige Konsequenzen für das chemische Milieu im Meeres-

boden. Die "Verbrennung" von Nahrung verursacht Sauerstoffzehrung im bodennahen Wasser. Bei zuviel Nahrung kommt es zu Sauerstoffmangel oder sogar zum völligen Sauerstoffschwund, der den Bestand der Bodentiere gefährdet.
Aufgrund der Änderung des Sauerstoffgehaltes ändern sich auch die chemischen Bedingungen im Meeresboden, so daß Stoffe in Lösung gebracht werden, die ihrerseits massiv die Vorgänge im Wasser beeinflussen. Hierzu gehören Pflanzennährstoffe wie Phosphat, aber auch Schwermetalle, die eine Vergiftung des Bodenwassers verursachen können. Der Nahrungseintrag aus dem Wasser beeinflußt innerhalb weniger Tage auch solche Organismen, die in der Tiefe des Meeresbodens leben. Nahrungspartikel werden von wühlenden Organismen vergraben. Auf ihrem Weg durch das Sediment werden die Partikel durch Bakterien an- und aufgelöst, so daß auch gelöste Substanzen anschließend tief in das Sediment transportiert werden. Auf diese Weise gelangt nach wenigen Tagen das Signal "frischer Nahrungsversorgung" von der Oberfläche bis in Tiefen von 10 cm und tiefer.
Die im Jahresverlauf ungleichmäßige Nahrungsversorgung hat zur Folge, daß der Stoffumsatz am Meeresboden nicht über die Messung der Sauerstoffzehrung ermittelt werden kann, wie es heute noch gängiges Verfahren in der Umweltüberwachung ist. Insbesondere in Phasen mit reduziertem Sauerstoffgehalt im Bodenwasser findet die Verbrennung der Nahrung zum Teil im freien Wasser statt. In der Kieler Bucht ist die Sauerstoffzehrung des Bodenwassers genauso groß wie die Zehrung des Meeresbodens selber. Gärungsprozesse finden statt, wobei Nahrung verwertet wird, ohne daß eine entsprechende Sauerstoffzehrung auftritt.
Selbst geringe Strömungsgeschwindigkeiten sind zehnmal größer als hohe Sinkgeschwindigkeiten, mit denen Nahrungspartikel im Wasser absinken. Unmittelbar über dem Meeresboden driften viel mehr Nahrungspartikel vorbei, als in einem vergleichbaren Zeitraum vertikal herabsinken würden.

Filtrierende Bodentiere nutzen diesen lateralen Partikelstrom. Sandklaffmuscheln am Boden der Kieler Bucht fangen pro Quadratmeter mehr Nahrung ein, als auf diese Fläche insgesamt herabsinkt. Das Nahrungsangebot kann auf diese Weise verdoppelt werden.
Im bodennahen Wasser kommt es zu einer Anreicherung von Partikeln, wegen der dort höheren Turbulenz. Die mit der Strömung lateral verdriftenden Partikel sammeln sich, der Schwerkraft folgend, in den tiefsten Bereichen der Kieler Bucht. Kurzfristig kann allerdings ein Sturm auch zum gegenteiligen Effekt führen und Material aus den tiefen Rinnen der Kieler Bucht zurück ins Flachwasser transportieren. Dort bleibt es jedoch nicht auf Dauer liegen. Vermutlich dauert es in der Kieler Bucht durchschnittlich 140 Jahre, bis ein Partikel auf Dauer im Sediment deponiert wird. Auch Partikel, die schon 20 cm im Meeresboden vergraben sind, können durch Bodentiere wieder zurück zur Oberfläche befördert werden. Sie könnten dann erneut aufgewirbelt werden. Erst Partikel, die noch tiefer vergraben werden, sind diesem Kreislauf entzogen. In den tiefsten Teilen der Kieler Bucht hat sich in den letzten 8000 Jahren durch das Herabsinken von pflanzlichen und mineralischen Partikeln eine mehr als 10 m dicke Schicht Sediment gebildet. Die lateralen Prozesse führten zu einer sehr unterschiedlichen Verteilung der Sedimente in der Kieler Bucht. In den tiefsten Teilen sammelt sich Schlick, an den Hängen sandiger Schlick, der die größte Artenvielfalt der Fauna und den größten Nahrungsverbrauch aufweist. In flacheren Gebieten findet sich Sand, der ständig umgelagert wird.
Das tatsächliche Nahrungsangebot für die Bodenorganismen im tieferen Bereich der Kieler Bucht ist durch laterale Transportprozesse etwa 4-5 mal größer als durch das 1973 entwickelte Modell von Hargrave beschrieben wird.

1. Introduction

Heterotrophic life in the aphotic benthic zone of the sea is based on primary production that takes place in the euphotic pelagic or benthic zones. Thus, the mere existence of the aphotic way of life is already proof for transport mechanisms that couple the primary production zones with exclusively secondary production habitats. Although during recent years with the detection of deep sea vents and subduction zones other energy and carbon sources for benthic life have been described, organic matter (OM) produced in the pelagial is the beginning of the benthic food web in most cases.
The flow of matter from the pelagial to the benthal was until the 1970's believed to occur as a steady rain of particles that settle to the sea floor (cf. Steele, 1974). However, already in 1940, Remane reported that the sediment, he collected in Kiel Bight during spring, was covered by a greenish layer derived from pelagic diatoms. This indicates that some imbalances may occur in the particle rain. In lakes, Jonasson (1964) described the influence of settling spring and autumn plankton blooms on the development of Chironomidae larvae in the sediment.
Qualitatively there was never any doubt about the dependence of benthic life on pelagic processes and the above statements may be regarded as trivial. Things grew complicated, however, when a quantitative description of benthic-pelagic coupling was tried. Hargrave (1973) described a model in which the pelagic primary production is related to the oxygen demand of the sediment; as a third variable he introduced the depth of the mixed layer in the water column.
The model was deduced from 20 published examples covering very different systems such as coastal

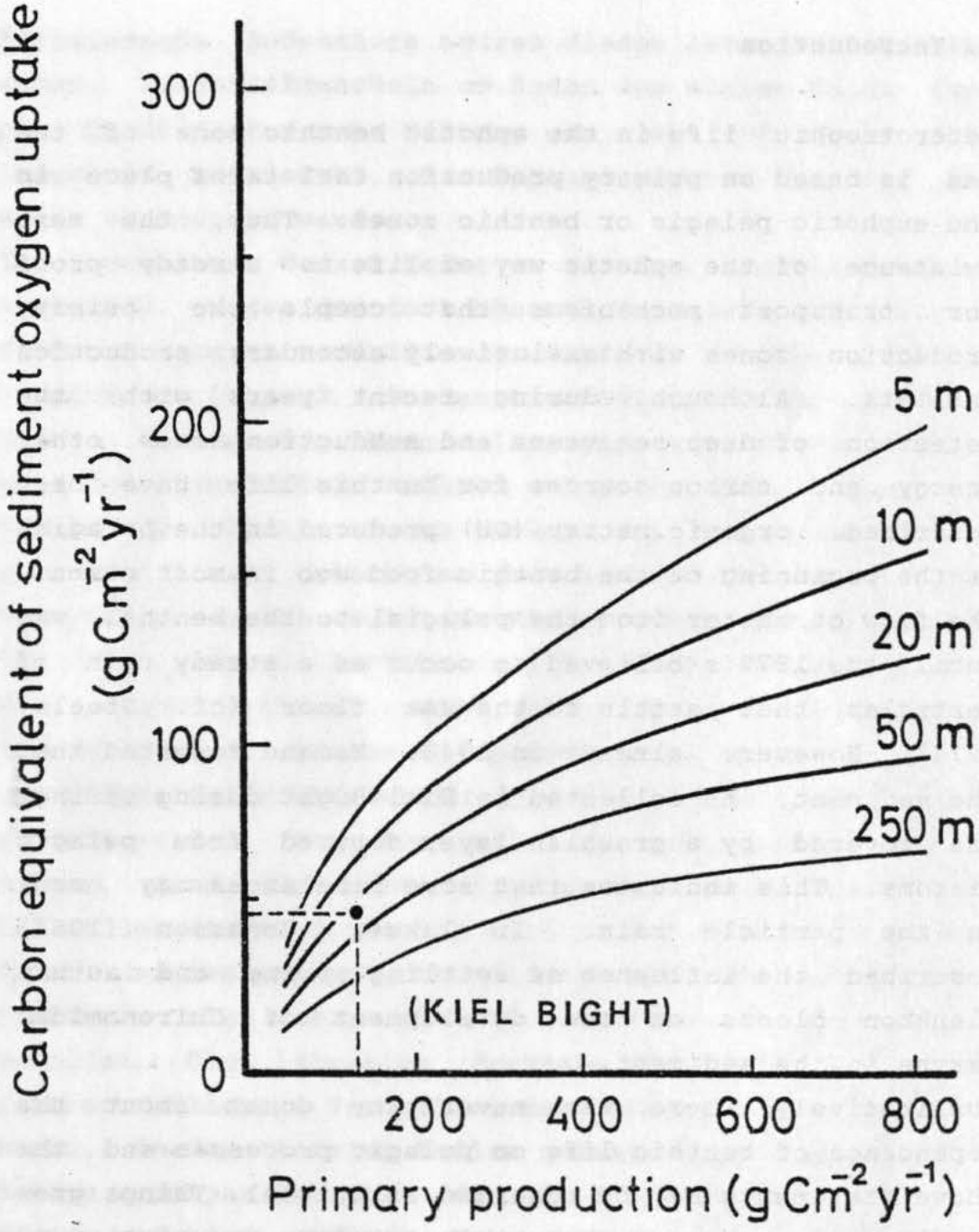

Fig. 1: Hargrave's model (1973) of benthic-pelagic coupling relates benthic oxygen consumption to surface primary production and to the mean annual mixed layer depth, using the equation $C_o = a(C_i)^b/(Z_m)^c$, where C_o = carbon equivalent of annual sediment oxygen uptake, C_i =annual primary production, Z_m=mixed layer depth, a,b,c = constants. The example of Kiel Bight is added according to data of von Bodungen (1975) and Pollehne (1986). Carbon equivalent of sediment oxygen consumption was taken from Boknis Eck (18-28 m water depth). Mixed layer depth in Kiel Bight is about 15 m during summer and 28 m during winter.

upwelling areas as well as fresh water lakes. Fig. 1 also includes the example of Kiel Bight based on data from von Bodungen (1975) and Pollehne (1986); their results fit perfectly into the model. The Hargrave model is based on an annual time scale and does not intend to give oxygen consumption rates of the sediment during shorter intervals, for example, during or after a spring bloom. Another model predicts organic matter content of the sediment from primary production, sedimentation rate and some sediment features such as porosity and density (Müller and Suess, 1979). Benthic oxygen demand was further estimated from the difference between carbon flux to the sediment minus burial rate in the sediment. The flux was given as

$$C_{flux(z)} = \frac{C_{prod}}{0.0238z+0.212}$$

$z \geq 50m$ water depth, C_{prod} = primary production (Suess, 1980).

A new approach in the study of benthic-pelagic coupling was started, when the plankton researchers at the end of the 1970's demonstrated pelagic succession patterns and discovered that certain species, especially diatoms, may settle rapidly creating a distinct annual sedimentation pattern. A review was recently given by Smetacek (1985a).

Sedimentation events taking only a few days create a coupling of pelagic to benthic processes on a very short time scale. Such processes demand from benthos researchers investigation on the same short time scale (Graf et al., 1982). It could be demonstrated that the benthic response to such pelagic events is immediate.

The investigation of a sedimentation event, for example

during a spring bloom, soon results in the finding that processes other than just a vertical flux of particulate organic matter (POM) are involved. Fig. 2 visualises these additional transport mechanisms.
An ideal investigation of a sedimentation event has to trace the pathway of particles from production to final geological deposition in the sediment. Proof has to be given that particles collected in a sediment trap have really been produced in the corresponding area above the trap and that the amount of collected matter equals the losses from the water column. To document sedimentation (S) it is necessary to demonstrate that the particles enter the nepheloid layer and reach the sea floor and that they become incorporated into the sediment. A reflux of particles or resuspension has to be considered and the extent to which currents and bottom topography of the area increase or diminish the sedimentation event by lateral advection (LA) has to be controlled. All this means that it is impossible to relate one square meter of the sea floor to one square meter of a water column.
The organic fraction of the particle input to the sediment is potential food for the benthic organisms. It is remineralized, and dissolved nutrients flow back to the water column (Smetacek and Pollehne, 1986; Balzer et al., 1987;). From the pelagic point of view this aspect of benthic-pelagic coupling is very interesting, because mineralized nutrients are the basis for new production in the euphotic zone. For the following argumentation, however, nutrients are of less importance, because inorganic nutrients rarely seem to limit heterotrophic life in the sediment.
For my argumentation I will focus on the sediment-water interface and consider a slice of sediment, for example, of 1 m^2 area and 1 cm sediment depth. The Hargrave and Suess models assume that particle flux to the sediment

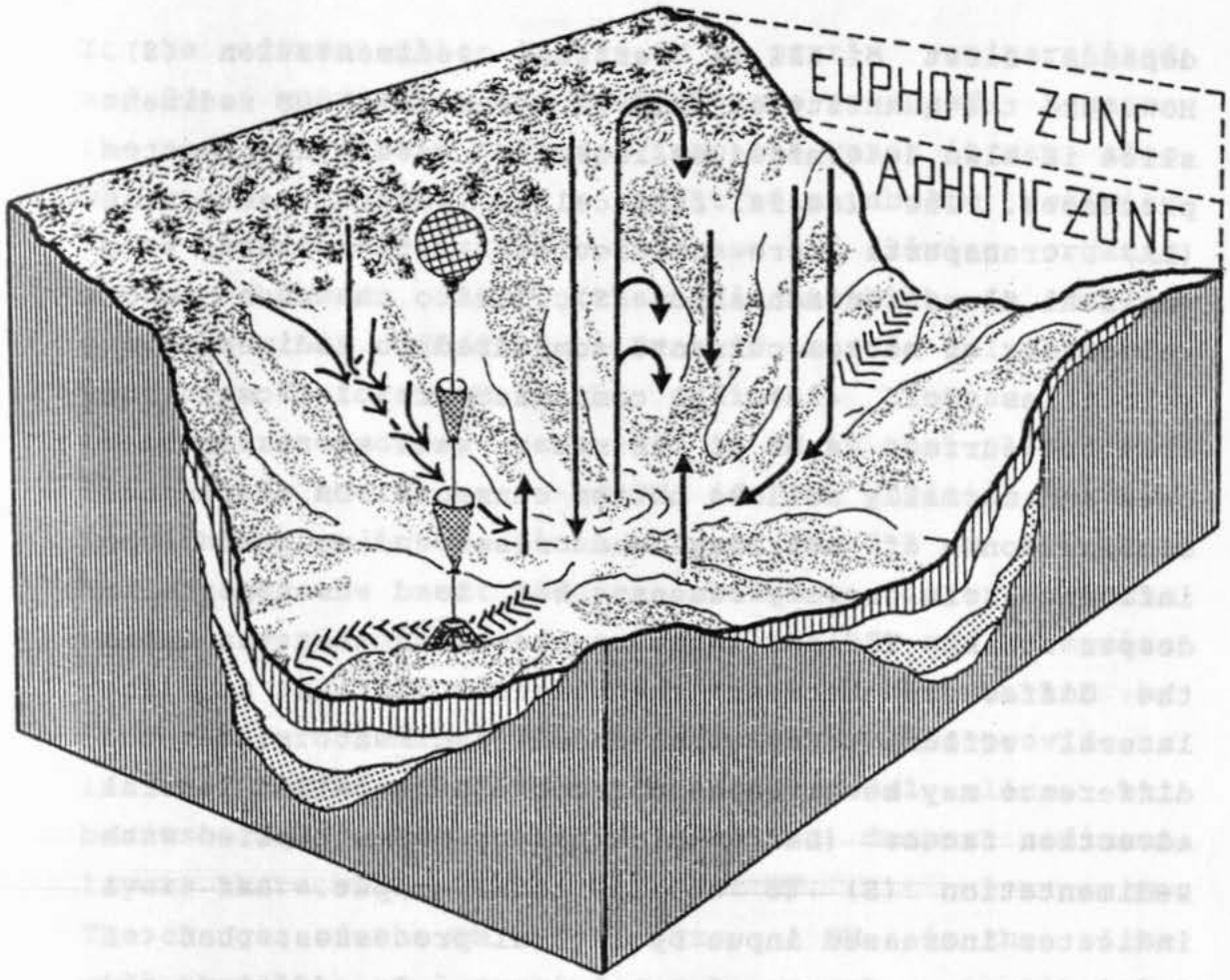

Fig. 2: Processes that determine the organic matter content of sediments in Kiel Bight. Sediment produced during the past 8000 years cover a pleistocene underground. The arrows indicate sedimentation, resuspension and lateral advection; the herring bone pattern indicates deep water currents following the channel system. The topography of the area allows geological deposition in deeper areas only.

depends first of all on vertical sedimentation (S). However, the quantity of this flux reaching our sediment slice is also determined by lateral, mostly near-bottom processes. The lateral flux called lateral advection (LA) transports more particulate matter than the vertical flux, sedimentation (S), due to the much higher velocities of bottom currents compaired to sedimentation velocities (cf. 4.3). LA contains particles settling from the surface layer of the sea as well as resuspended ones and normally follows bottom currents. On slopes the combination of settling and resuspending and the influence of gravity causes a bed load transport to deeper areas. The net input to a certain area via LA is the difference between the lateral influx and the lateral efflux. For the model sediment slice the difference may be given as a factor, here called lateral advection factor (Laf), which has to be multiplied with sedimentation (S) to obtain total input. Laf > 1 indicates increased input by lateral processes; Laf < 1 > 0 indicates a decreased total input. In addition, the suspension feeding fauna is actively removing particles from the water column. The process is called biodeposition (BD), when feces are deposited on or in the sediment. In most cases an influx of dissolved organic matter (DOM) from the water column to the sediment can be neglected, because concentrations in the pore water are much higher. On the contrary this gradient will cause an efflux of DOM by diffusion, an effect which may be increased by biopumping of the fauna. The losses of OM from the sediment slice into the water, here summarized as efflux (EF), include in the liquid phase DOM and as decomposition products dissolved inorganic nutrients. In the solid phase, losses are by resuspension, which either has physical origins (erosion) or is caused by animals (bioentrainment).

In the sediment slice itself OM is partly remineralized and CO_2, nutrients and heat (Q) are produced. Because the heat is finally released into the water it can also be given as a flux. As a result of metabolic activity there is an increase or decrease of living organic matter (biomass, B) in the sediment which is called production (P), dB/dt=P. Even if this is only a minor portion of total OM in the sediment, biomass is an important temporary reservoir of OM in the slice and diminishes the decrease of OM, if P is positive.
There are also interactions between the 0-1 cm sediment slice and the next deeper sediment layer. These processes are summarized as down flux (DF) and comprise particle and liquid transport by bioturbation and by diffusion processes. The same processes also provide an influx from deeper layers into the model slice, but because OM is also remineralized in deeper sediment layers there will mostly be a net DF.
The changes of the OM - pool size, Δ OM, in the slice will thus be

$$\Delta \text{ OM} = \text{Laf}*S + BD - EF - DF - Q - P.$$

Because for most of the above fluxes and rates no mathematical terms can be given, a time function of OM is not yet possible. Only under steady state conditions may parts of EF and DF be calculated via Fick's law; for P many approaches are available. A much simpler model was presented by Westrich and Berner, 1984, who suggested a first order decay of OM

$$d \text{ OM}/dt = -k*\text{OM}.$$

Several authors tried to determine the decay constant k (Grant and Hargrave, 1987; Kristensen and Blackburn,

1987). This approach, however, needs an enclosed sediment slice excluding exchange processes, which is not realistic for natural sediments.

OM comprises a non reactive, refractory fraction (OM_r), which has already reached the maximum degree of degradation, a more or less labile fraction (OM_l) representing the food resource, and the living part of OM (biomass, B). All these fractions may be exchanged by EF and DF. Only in the deepest bioturbated layer (sediment slice), is the particulate fraction of non reactive OM (OM_r) equivalent to the particulate geological deposition. Fluid exchange via diffusion reaches as deep as pore water is available and microbial degradation of labile OM continues.

Fig. 3 summarizes the fluxes for a model sediment slice in a boreal system with a distinct annual sedimentation pattern such as in Kiel Bight, Western Baltic Sea. During spring and autumn lateral advection factor times sedimentation (Laf*S) is high, followed by a high heat release (Q) and a positive production (P>Ø). During autumn, macrofauna activity is enhanced; biodeposition (BD), down flux (DF) and efflux (EF) are much more significant. During summer Laf*S is less important, but BD reaches its annual maximum. During winter all biological processes are smaller, whereas physical effects cause relatively high S and EF.

This simple model depicts that very different combinations of fluxes may occur during the annual cycle. It also indicates that an equilibrium of all fluxes or a steady state i.e.,

$$d\,OM/dt = Ø,$$

is not likely to occur, when the time scale is less than one or even a few years.

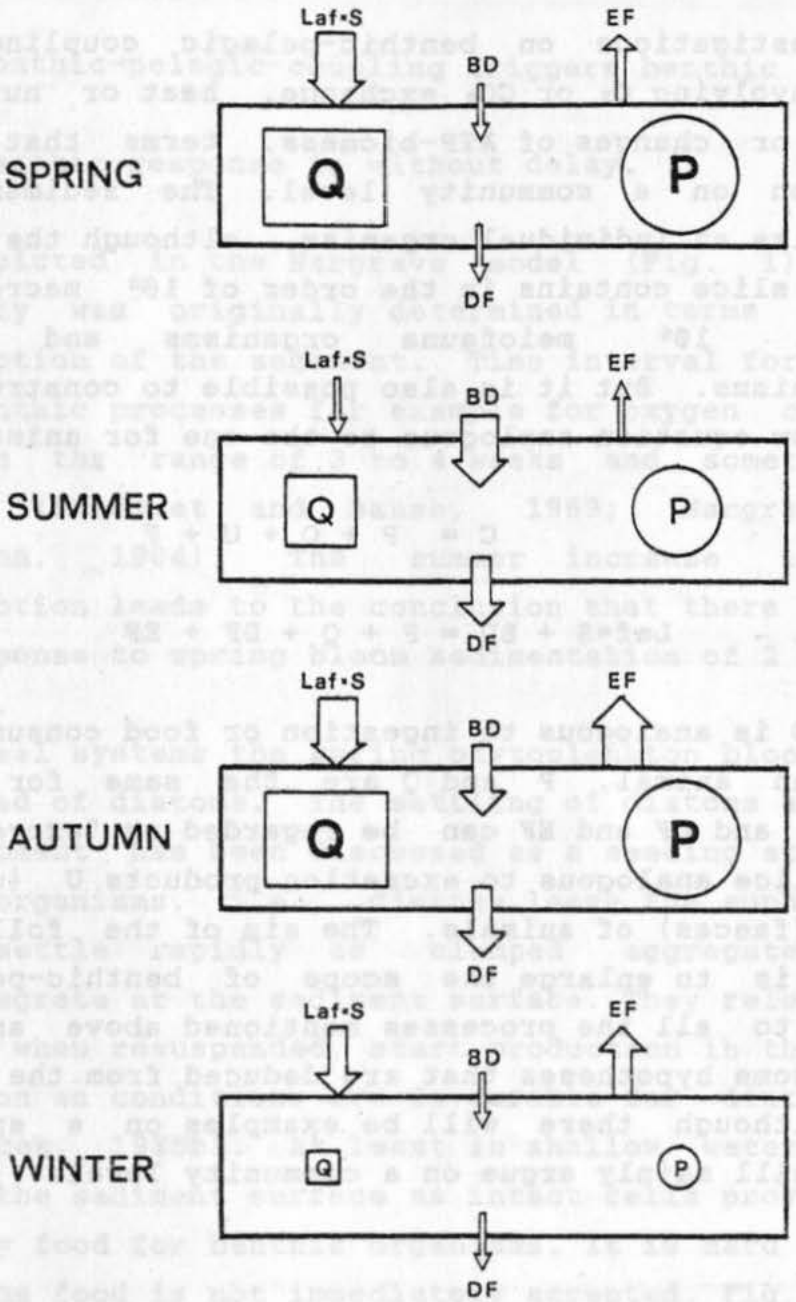

Fig. 3: Seasonal variability of processes that determine the organic matter content in the surface sediment slice (0-1 cm). Laf=Lateral advection factor, S=Sedimentation BD=Biodeposition, EF=Efflux comprising all losses of OM in a liquid or particulate form into the water, Q=Heat Release, P=Production, DF=Downward Flux, comprising all losses to deeper sediment layers. The differences in size of the symbols indicate the relative importance of the processes for each season. The symbols do not depict that the ratio between Q and P will also differ during the seasons.

Many investigations on benthic-pelagic coupling use methods involving O_2 or CO_2 exchange, heat or nutrient release, or changes of ATP-biomass, terms that give information on a community level. The sediment is treated like an individual organism, although the model sediment slice contains in the order of 10^3 macrofauna organisms, 10^6 meiofauna organisms and 10^{13} microorganisms. But it is also possible to construct an energy flow equation analogous to the one for animals:

$$C = P + Q + U + F$$

$$Laf*S + BD = P + Q + DF + EF$$

Laf*S + BD is analogous to ingestion or food consumption (C) of an animal, P and Q are the same for both equations and DF and EF can be regarded as "excretion" of the slice analogous to excretion products U (urine) and to F (faeces) of animals. The aim of the following synopsis is to enlarge the scope of benthic-pelagic coupling to all the processes mentioned above and to discuss some hypotheses that are deduced from the flux model. Although there will be examples on a species level, I will mainly argue on a community level.

2. Benthic-pelagic-coupling triggers benthic life.

2.1 Benthic response is without delay.

As depicted in the Hargrave model (Fig. 1), benthic activity was originally determined in terms of oxygen consumption of the sediment. Time interval for the study of benthic processes for example for oxygen consumption was in the range of 3 to 4 weeks and sometimes even larger (Pamatmat and Banse, 1969; Hargrave, 1978; Wassmann, 1984). The summer increase of oxygen consumption leads to the conclusion that there is a delay in response to spring bloom sedimentation of 2 weeks to 2 months.

In boreal systems the spring phytoplankton bloom is often composed of diatoms. The settling of diatoms after bloom development has been discussed as a seeding strategy of these organisms, i.e., diatoms leave the euphotic zone and settle rapidly as clumped aggregates, which disintegrate at the sediment surface. They release spores which, when resuspended, start production in the pelagial as soon as conditions are favourable for diatoms again (Smetacek, 1985b). At least in shallow waters diatoms reach the sediment surface as intact cells providing high quality food for benthic organisms. It is hard to imagine that the food is not immediately accepted. Fig. 4 depicts a response in terms of heat production and Electron-Transport-System (ETS) activity within less than 6 days to a spring bloom sedimentation event at the end of March. In the following years response to spring bloom sedimentation was observed in four case studies (Fig. 5 a-d). In Kiel Bight diatoms settle from mid-March to the end of March (Smetacek, 1980). The late increase of heat production in 1984 and 1986 was due to delayed bloom development. The reasons for delay were easterly storms

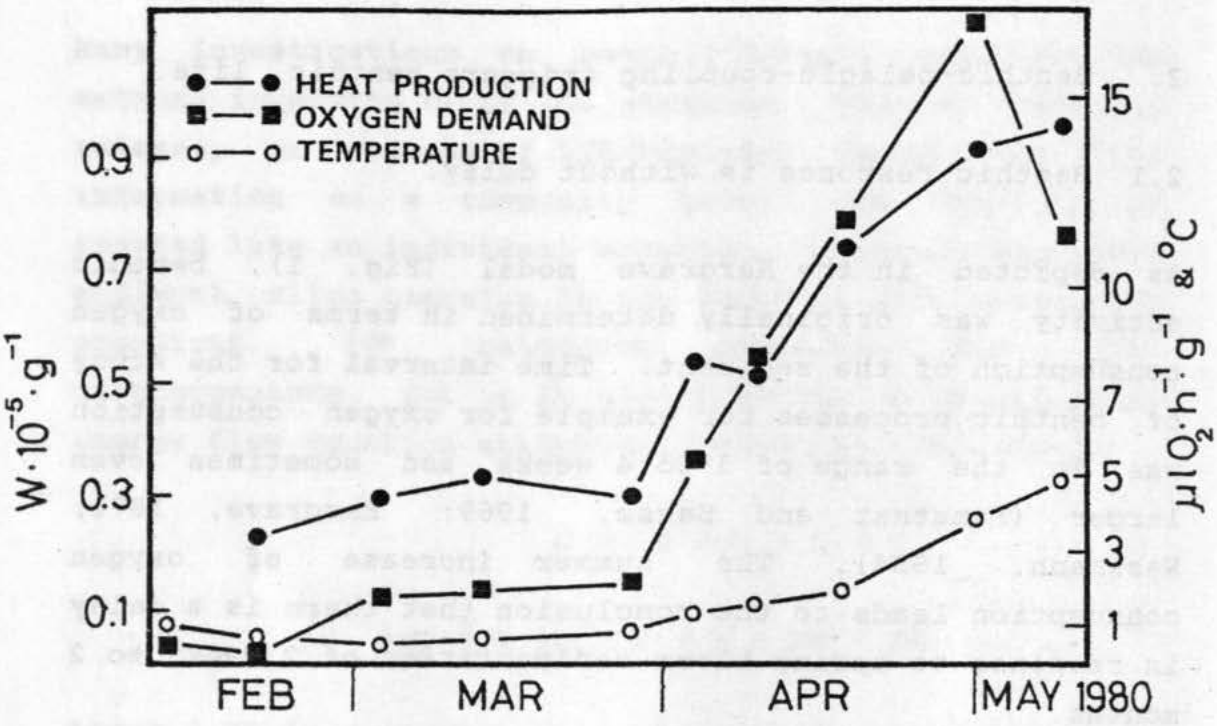

Fig. 4: First evidence of an immediate response to a spring bloom sedimentation event in 1980. Settling diatoms reached the seafloor at the end of March. In this study oxygen consumption (µl O_2 $h^{-1}g^{-1}$) of the 0-1 cm layer was determined as Electron-Transport-System (ETS) activity, which also comprise anaerobic respiration. Heat production is given in Watt ($W = J\ s^{-1}$) per g sediment d.w.. Temperature increase from mid-March to mid April is less than 2 °C (Redrawn after Graf et al., 1982).

in 1984 causing an interruption of bloom development and long lasting ice coverage in 1986, which caused a 4 week delay.

Response to autumn phytoplankton bloom sedimentation events was also within less than one week. In field studies with 1 week sampling intervals sometimes only one increased value for heat production was detectable (Graf et al., 1983; Czytrich et al., 1986). Food pulse

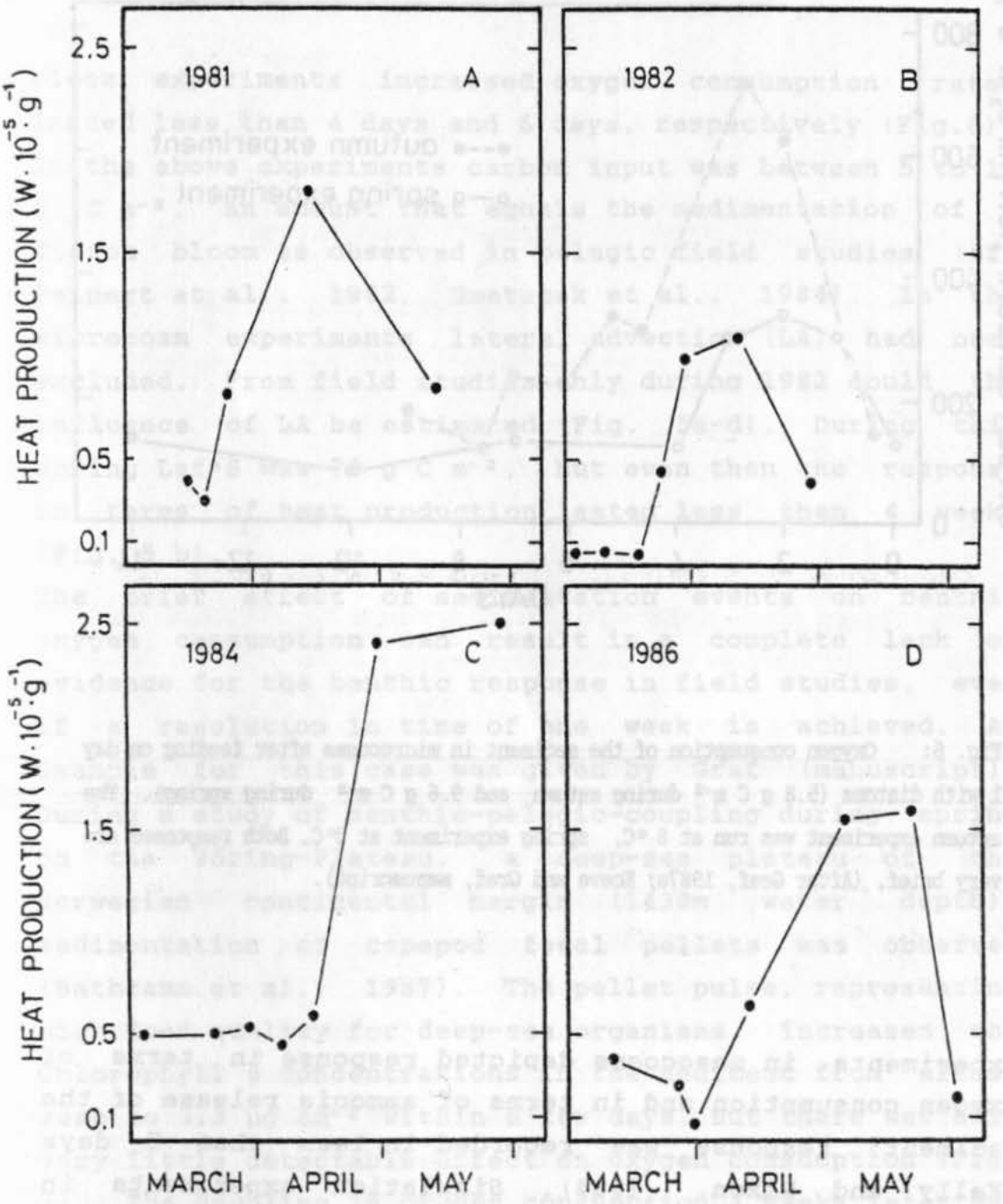

Fig. 5: Four case studies of response to spring phytoplankton bloom sedimentation in terms of heat production of the sediment surface (0-1 cm). A - C depict studies from Boknis Eck, (17-20 m water depth, Western Kiel Bight, Baltic Sea), D is from central Kiel Bight (17 m water depth). (A after Schulz, 1983; B after Graf et al., 1983; C Graf, unpublished data; D Eversberg and Graf, unpublished data).

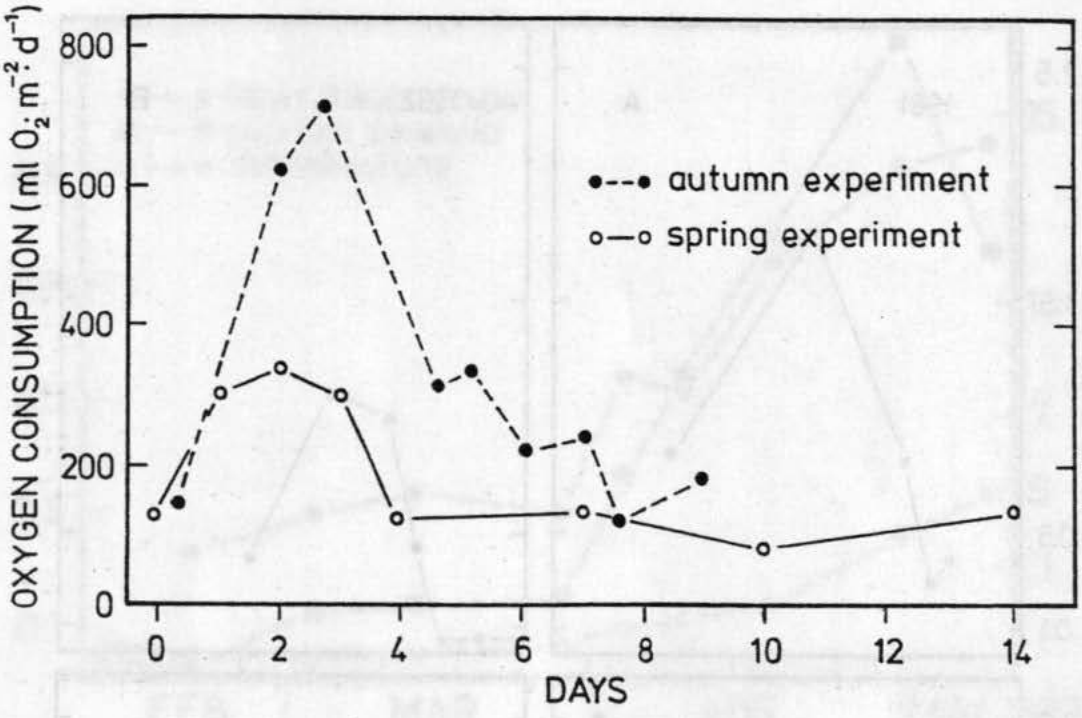

Fig. 6: Oxygen consumption of the sediment in microcosms after feeding on day 1 with diatoms (5.8 g C m^{-2} during autumn and 9.6 g C m^{-2} during spring). The autumn experiment was run at 8 °C, spring experiment at 3°C. Both responses are very brief. (After Graf, 1987a; Koeve and Graf, manuscript).

experiments in mesocosms depicted response in terms of oxygen consumption and in terms of ammonia release of the sediment; response was recorded in less than 5 days (Kelly and Nixon, 1984). Simulation experiments in microcosms proved that response is even faster. Fig. 6 gives oxygen consumption of the sediment in microcosms stimulated by the addition of fresh diatom cells (Graf, 1987a; Koeve and Graf, manuscript). Increase in oxygen consumption within one day of bloom sedimentation is by a factor of 4-5 during autumn and 3-4 during spring.

On the other hand the reponse in terms of oxygen consumption is very brief. During the spring and autumn

bloom experiments increased oxygen consumption rates lasted less than 4 days and 6 days, respectively (Fig.6). In the above experiments carbon input was between 5 to 10 g C m^{-2}, an amount that equals the sedimentation of a diatom bloom as observed in pelagic field studies (cf. Peinert et al., 1982, Smetacek et al., 1984). In the microcosm experiments lateral advection (LA) had been excluded. From field studies only during 1982 could the influence of LA be estimated (Fig. 5a-d). During this spring Laf*S was 70 g C m^{-2}, but even then the response in terms of heat production lasted less than 4 weeks (Fig. 5 b).

The brief effect of sedimentation events on benthic oxygen consumption can result in a complete lack of evidence for the benthic response in field studies, even if a resolution in time of one week is achieved. An example for this case was given by Graf (manuscript). During a study of benthic-pelagic-coupling during spring on the Vöring-Plateau, a deep-sea plateau of the Norwegian continental margin (1430m water depth), sedimentation of copepod fecal pellets was observed (Bathmann et al., 1987). The pellet pulse, representing high food quality for deep-sea organisms, increased the Chlorophyll *a* concentrations in the sediment from almost zero to 3.3 µg cm^{-2} within a few days. But there was only very little detectable effect on oxygen consumption (Fig. 7). The doubling in oxygen consumption 4 weeks later was induced by summer sedimentation which increased the POC flux to sediment traps by a factor of 15 (Peinert et al., 1987). This example indicates a seasonal effect on benthic metabolism also in the deep-sea, as was already detected by Smith and Baldwin (1984) for the North Pacific. It seems that the response in the deep-sea is as fast as in shallow waters (cf. 2.4).

In field studies that try to follow the real time scale

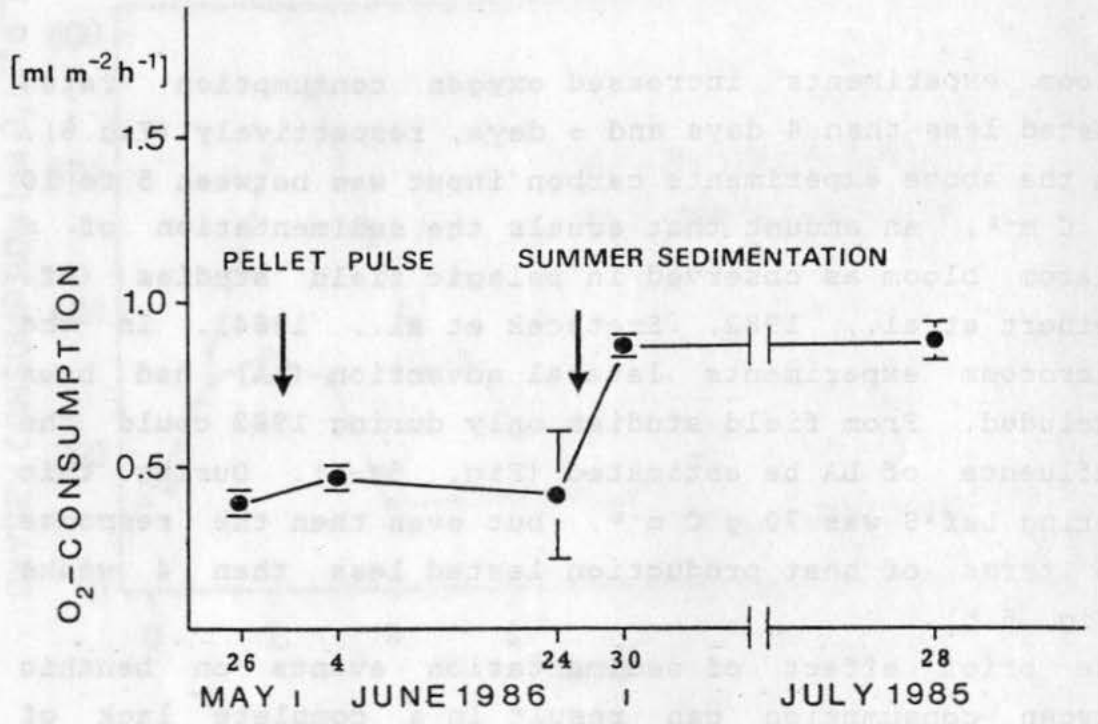

Fig. 7: Oxygen consumption of the deep-sea sediment from the Vöring-Plateau (Norwegian Sea, 1430 m water depth). Most likely the response to a pellet pulse has been missed. An increase of summer sedimentation rates by a factor of 15 was measured in sediment traps; this increase doubled oxygen consumption of the sediment. (After Graf, manuscript).

of benthic-pelagic coupling one must be prepared for the expected events and must sample every day. An example for such a study was given by Schulz (1983). In the Central Baltic Sea (BOSEX area, 56°18 N|18°34 E) benthic response in 80 m water depth to two distinct sedimentation events was described. The first event was in the form of a pulse of pellets derived from grazing zooplankton and the second as sedimentation of the bloom itself (Fig. 8). Both inputs significantly increased heat production in the sediment within one day.

Metabolic processes depend on temperature. In Kiel Bight

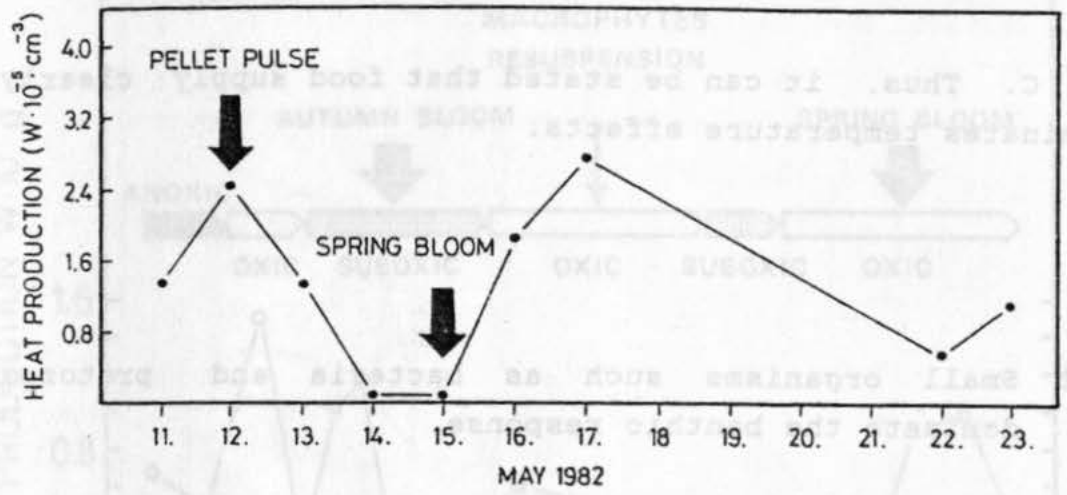

Fig. 8: Heat production of the sediment surface (0-1 cm) in the BOSEX area (Central Baltic Sea, 80 m water depth 56°18 N|18°34E). Reponse to a copepod fecal pellet pulse and to a spring phytoplankton bloom sedimentation is seen within one day (After Schulz, 1983).

at sediment stations in 20 m water depth a difference of up to 14 °C may occur between February and September (Krey et al., 1978). The seasonality in oxygen consumption in boreal seas is related to the annual temperature cycle and excellent correlations were found (cf. Wassmann, 1984; Hargrave and Phillips, 1986). Pamatmat and Banse, however, stated already in 1969 that only 30% of the variability in oxygen consumption of sediments could be explained by temperature effects. During spring bloom sedimentation events benthic activity was increased by a mean factor of about 7 (Fig. 4;5a-d), whereas temperature increase in the corresponding period was only 1 to 2 °C at temperatures of 0 to 3 °C. Q_{10} values for the Kiel Bight sediments were found to be 3-4 (Bengtsson, 1982; Graf, 1986). The effect of food input is comparable to the effect of a temperature increase of

20 °C. Thus, it can be stated that food supply clearly dominates temperature effects.

2.2 Small organisms such as bacteria and protozoa dominate the benthic response.

An increase of benthic biomass is the result of increased benthic metabolism. On the community level ATP-concentrations are taken as an overall parameter of biomass. In field studies ATP-biomass increased on the same time scale as heat production (Fig. 9). How close heat release and ATP-biomass increase are related is depicted in Fig 10. In a simulation experiment for the sedimentation of an autumn phytoplankton bloom ATP-development is exactly in phase with heat production. Both parameters reach maximum values in the top sediment layers on day 6. Therefore it can be stated that a biomass response is also immediate.

The ATP-method extracts nucleotides from sediment cores which contain bacteria, protozoans and the temporary as well as the permanent meiofauna. Thus the question arises as to which group of organisms is mainly responsible for the observed rapid increase of biomass and what is the response by macrofauna?

An immediate response of bacterial biomass to sedimentation events was demonstrated by Meyer-Reil (1983), as evidenced by division of cells as well as by growth of individual cells. This process leads to a shift of the bacterial size spectrum. Such an effect of settling phytoplankton blooms on the benthic bacterial population was recently shown for a muddy sediment in Kiel Bight, as depicted in Fig. 11. Autumn as well as

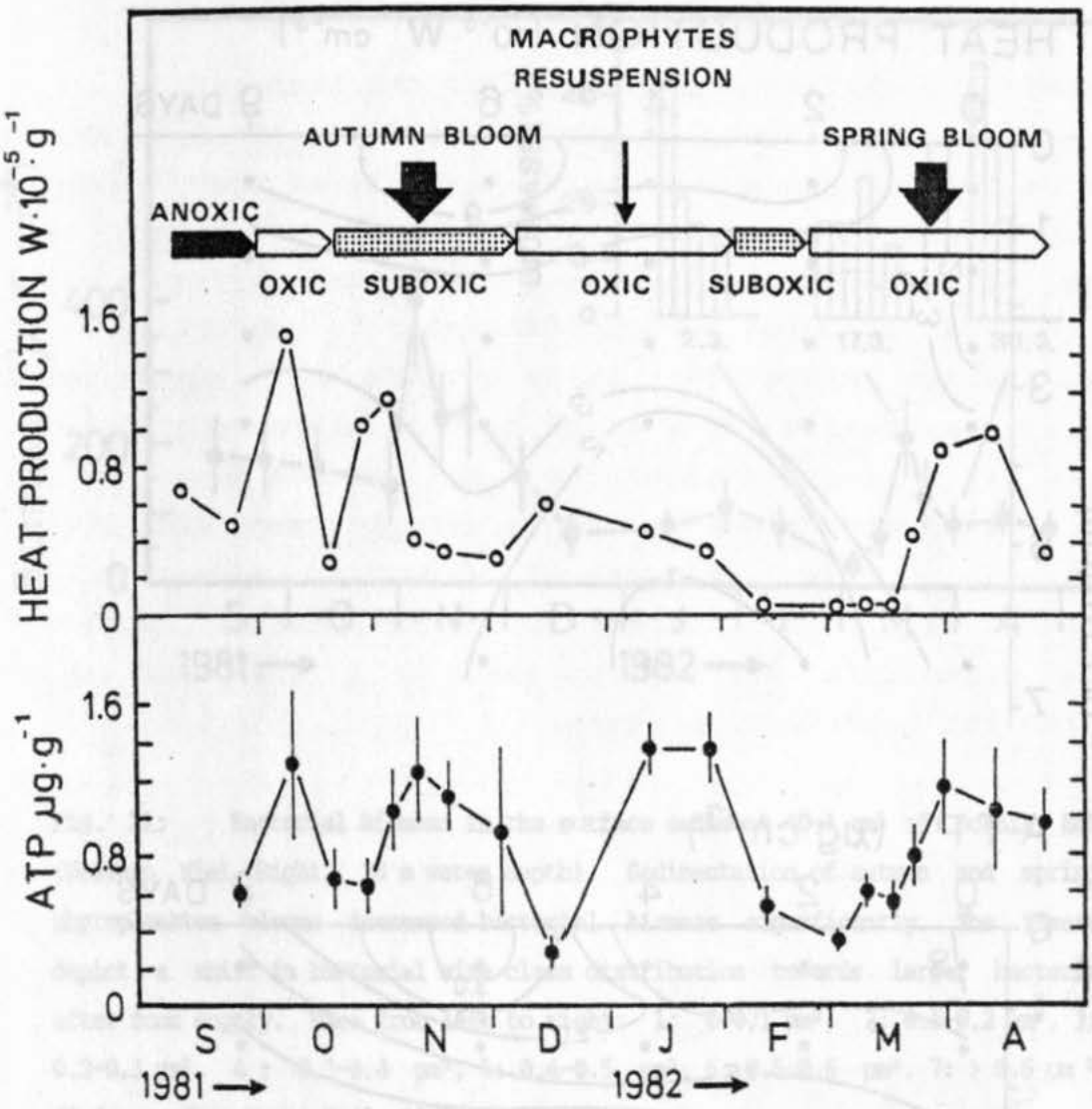

Fig. 9: Heat production and ATP-biomass in the sediment surface (0-1 cm) from Boknis Eck (Kiel Bight, 18 m water depth). The figure depicts responses to autumn and spring phytoplankton bloom sedimentation, but also to other events such as macrophyte input and break up of summer anoxia. Response in terms of ATP-biomass is as fast as in terms of heat production and is mainly achieved by bacterial and protozoan production. The decrease of ATP-biomass shortly after the decline in heat production indicates that bacteria and protozoans were grazed by other organisms (Redrawn after Graf et al., 1983).

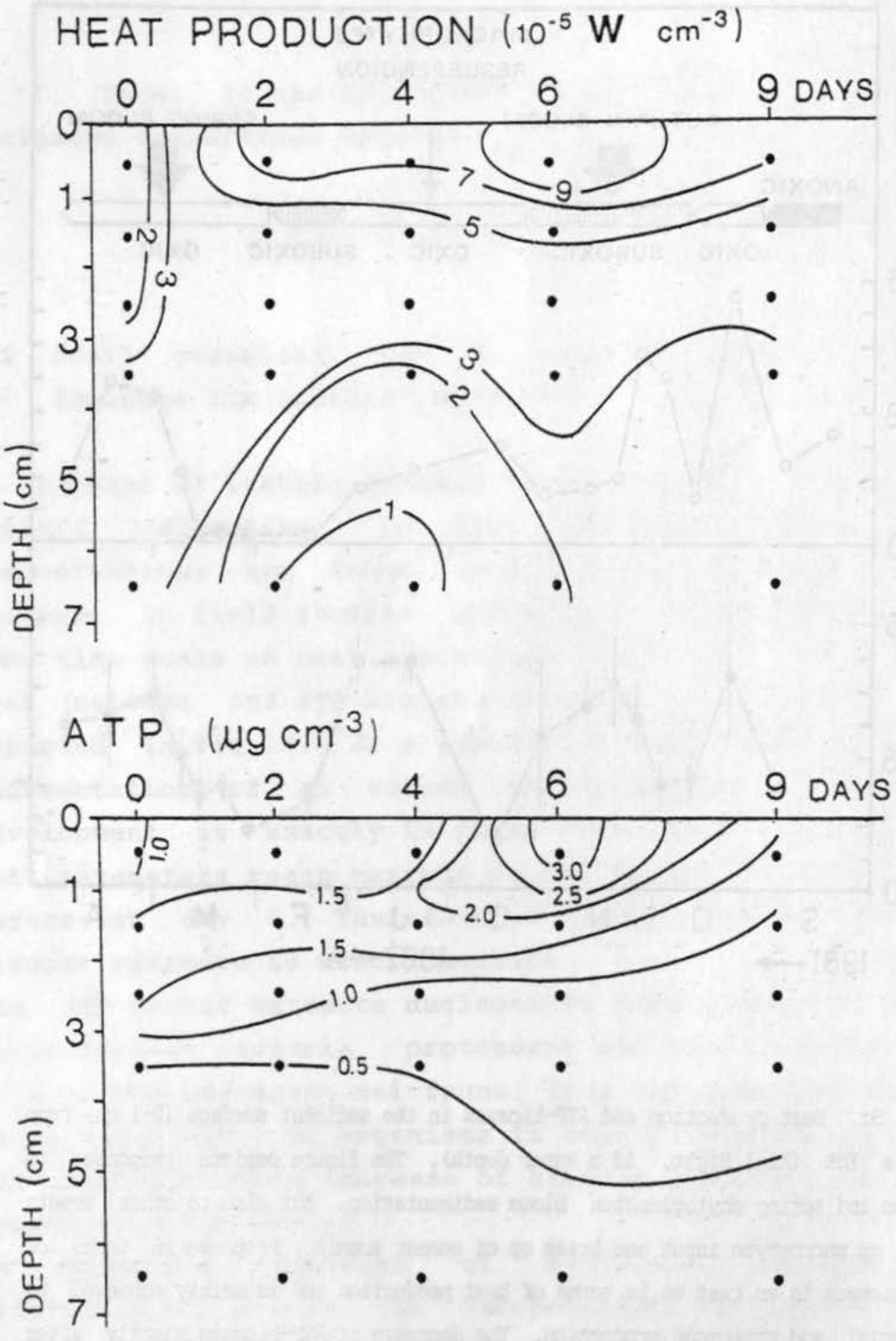

Fig. 10: Heat production and ATP-biomass during an experimental simulation of an autumn phytoplankton bloom sedimentation. Cultivated diatoms were added on day 1. Heat production and ATP-biomass develop in phase and reach maxima on day 6 (After Graf, 1987a).

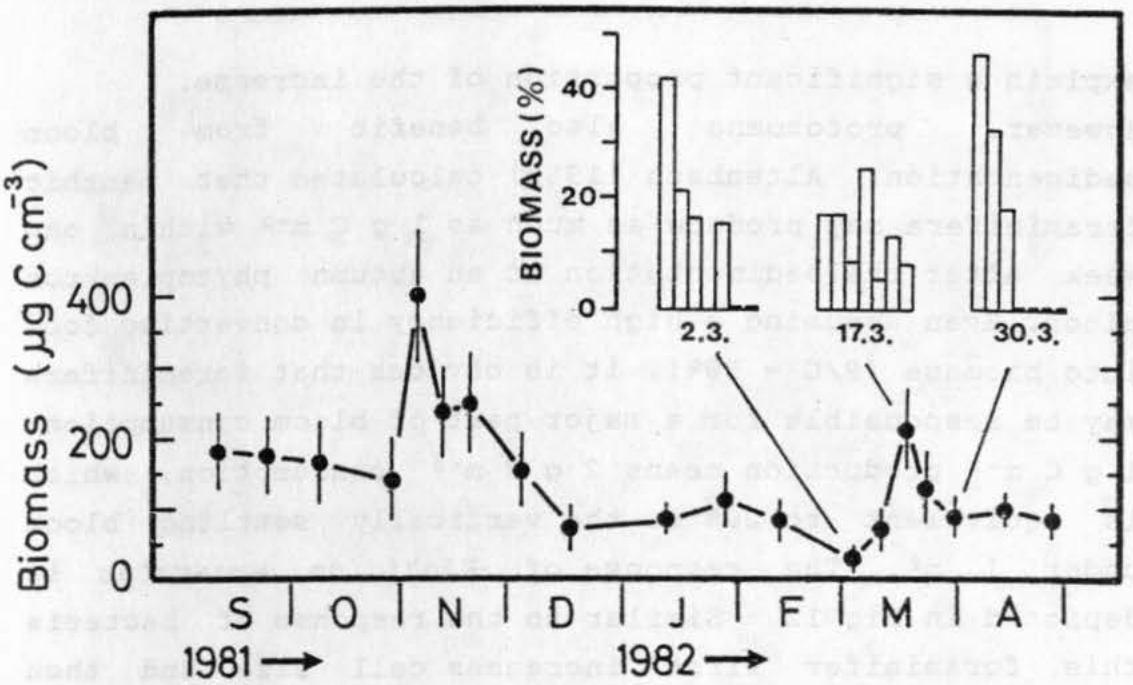

Fig. 11: Bacterial biomass in the surface sediment (0-1 cm) of Boknis Eck (Western Kiel Bight, 28 m water depth). Sedimentation of autumn and spring phytoplankton blooms increased bacterial biomass significantly. The insets depict a shift in bacterial size class distribution towards larger bacteria after food supply. Bars from left to right: 1: 0-0,1 µm³, 2: 0.1-0.2 µm³, 3: 0.2-0.3 µm³, 4 : 0.3-0.4 µm³, 5: 0.4-0.5 µm³, 6: 0.5-0.6 µm³, 7: > 0.6 µm³ (Redrawn after Meyer-Reil, 1987b).

spring phytoplankton blooms increased bacterial biomass by a factor of 2 to 3 (Meyer-Reil, 1987a). The size spectrum of bacteria during the spring bloom period shifted towards larger cells.

During the autumn phytoplankton bloom period in 1982 bacterial biomass increase was about 100 µg C cm^{-3} (Meyer-Reil, 1983). Assuming a C : ATP ratio of 250 an increase of 400 ng ATP cm^{-3} can be calculated. During this sedimentation event 600 ng cm^{-3} ATP increase was observed (Graf et al. 1983), so that bacteria might

explain a significant proportion of the increase. However, protozoans also benefit from bloom sedimentation. Altenbach (1985) calculated that benthic foraminifera may produce as much as 1 g C m^{-2} within one week after the sedimentation of an autumn phytoplankton bloom. Even assuming a high efficiency in converting food into biomass (P/C = 50%), it is obvious that foraminifera may be responsible for a major part of bloom consumption. 1 g C m^{-2} production means 2 g C m^{-2} consumption, which is equivalent to 20% of the vertically settling bloom under 1 m^2. The response of *Elphidium excavatum* is depicted in Fig 12. Similar to the response of bacteria this foraminifer first increases cell size and then starts the reproduction phase.

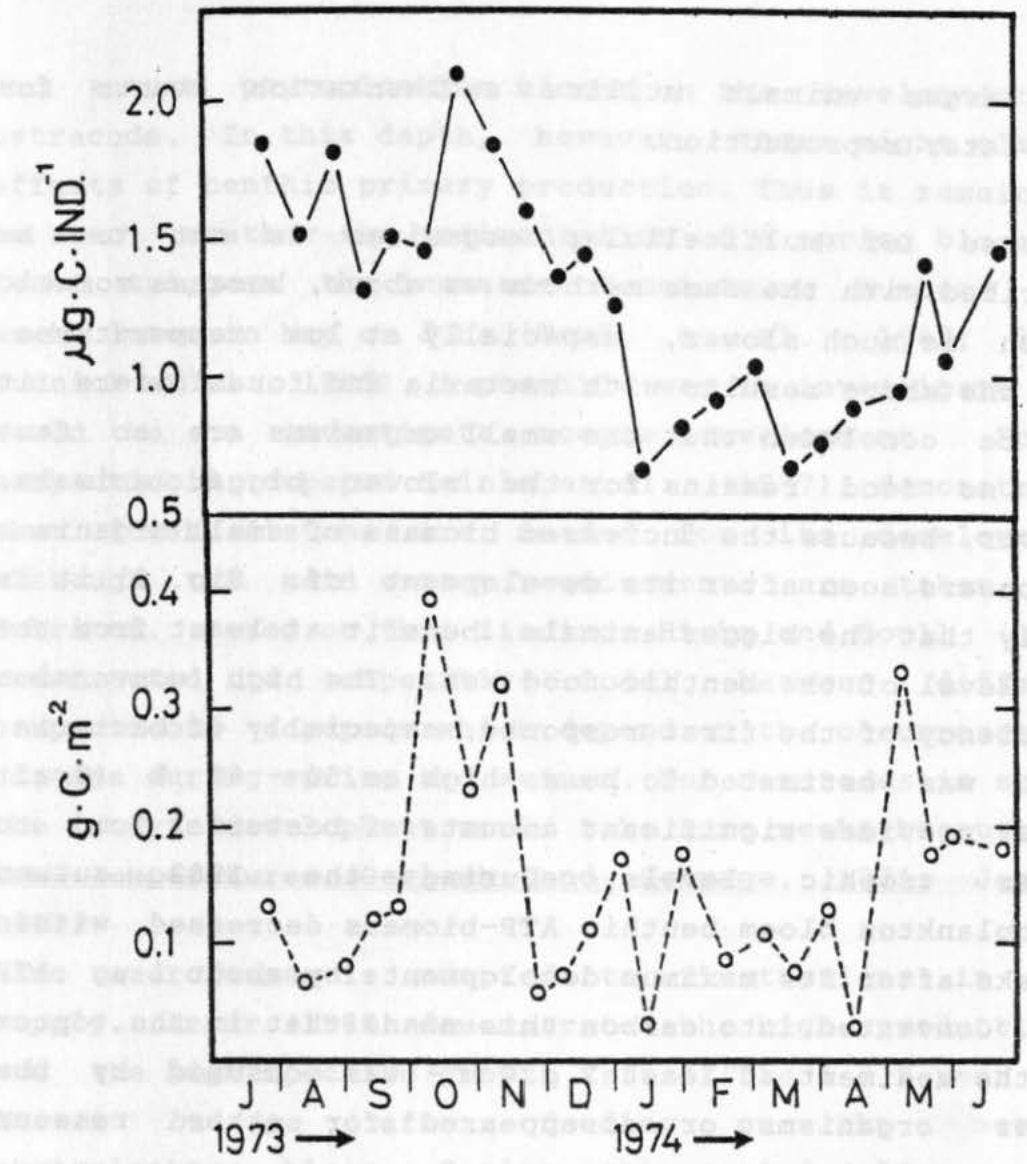

Fig. 12: Individual body mass and biomass of a population of the foraminifera *Elphidium excavatum* from Boknis Eck (Western Kiel Bight, 27m water depth). The autumn phytoplankton bloom 1973 was during early October, and the spring phytoplankton bloom 1974 during March (Redrawn after Altenbach, 1985).

2.3 Larger animals utilize sedimentation events for later reproduction.

Response of multicellular organisms is not to be described with the same methods as above, because somatic growth is much slower, especially at low temperatures. From the above results with bacteria and foraminifera it may be concluded that the small organisms are so fast that no food remains for the slower bigger animals. However, because the increased biomass of small organisms disappears soon after its development (cf. Fig. 9) it is likely that the bigger animals benefit at least from the next level of the benthic food web. The high conversion efficiency of the first response, especially of bacteria, which was estimated to be as high as 50 - 60 % (Graf, 1987a) provides significant amounts of bacterial food to higher trophic levels. During the 1982 autumn phytoplankton bloom benthic ATP-biomass decreased within 4 weeks after its maximum development by about 1 µg ATP cm^{-3}. Converted into carbon this means that in the top cm of the sediment at least 2 g C m^{-2} was consumed by the larger organisms or disappeared for other reasons (resuspension).

In shallow euphotic benthic habitats a tight coupling of benthic primary production to meiofauna development has been observed (Muus, 1967; Faubel and Meyer-Reil, 1983, Jensen, 1981; 1984). In deeper aphotic sediments on the other hand there is only little proof that sedimentation events have an effect on meiofauna. Juario (1975) described increasing abundance of nematodes for a 35 m North Sea station in early summer, which might be related to bloom sedimentation in this sea (cf. Davies and Pain, 1984). However, the observed effects were not very significant. For a 13 m station in the western part of Kiel Bight Rosenfeld (1979) observed an effect of spring

and autumn phytoplankton blooms on the development of ostracods. In this depth, however, there might also be effects of benthic primary production. Thus it remains to be seen, whether the sedimentation of a spring bloom at least triggers the increase of meiofauna numbers some weeks later in May or June (Graf, et al., 1982; 1984; Rudnick et al., 1985). A possible way to investigate this would be to investigate oocyte development. For a harpacticoid copepod Heinle et al. (1977) demonstrated that fresh diatoms are needed for its development, although the main energy requirements are taken from detritus. Based on this findings Hicks and Coull (1983) constructed a competitive model between different harpacticoid copepods which depend on the occurrence of diatoms during spring and autumn. For nematodes in spring the oocyte development would take some weeks because of low temperatures (Gerlach and Schrage, 1971; Jensen, 1983).

Also macrofauna is adapted to fluctuations in food supply. Ankar (1980) demonstrated the high productivity and the high specific growth rate of the 1 - 2 year old *Macoma baltica* after feeding on the settled phytoplankton bloom. During this period glycogen and lipid reserves are built up (Fig. 13; Graf et al., 1982). A smaller and more delayed effect was observed in the errant polychaete *Nephtys spec.*, a carnivore. For *Macoma baltica* the energy supply which has been accumulated in spring is a prerequisite for gamete production later during June and July (Ankar, 1980). The same may hold true for other species. For the most important macrofauna species in Kiel Bight, *Arctica islandica*, a spring and an autumn cohort can be distinguished, and the larval settlement of the polychaete *Pectinaria koreni* seems to be timed so that the autumn cohort can significantly benefit from the autumn bloom (Rumohr, 1980).

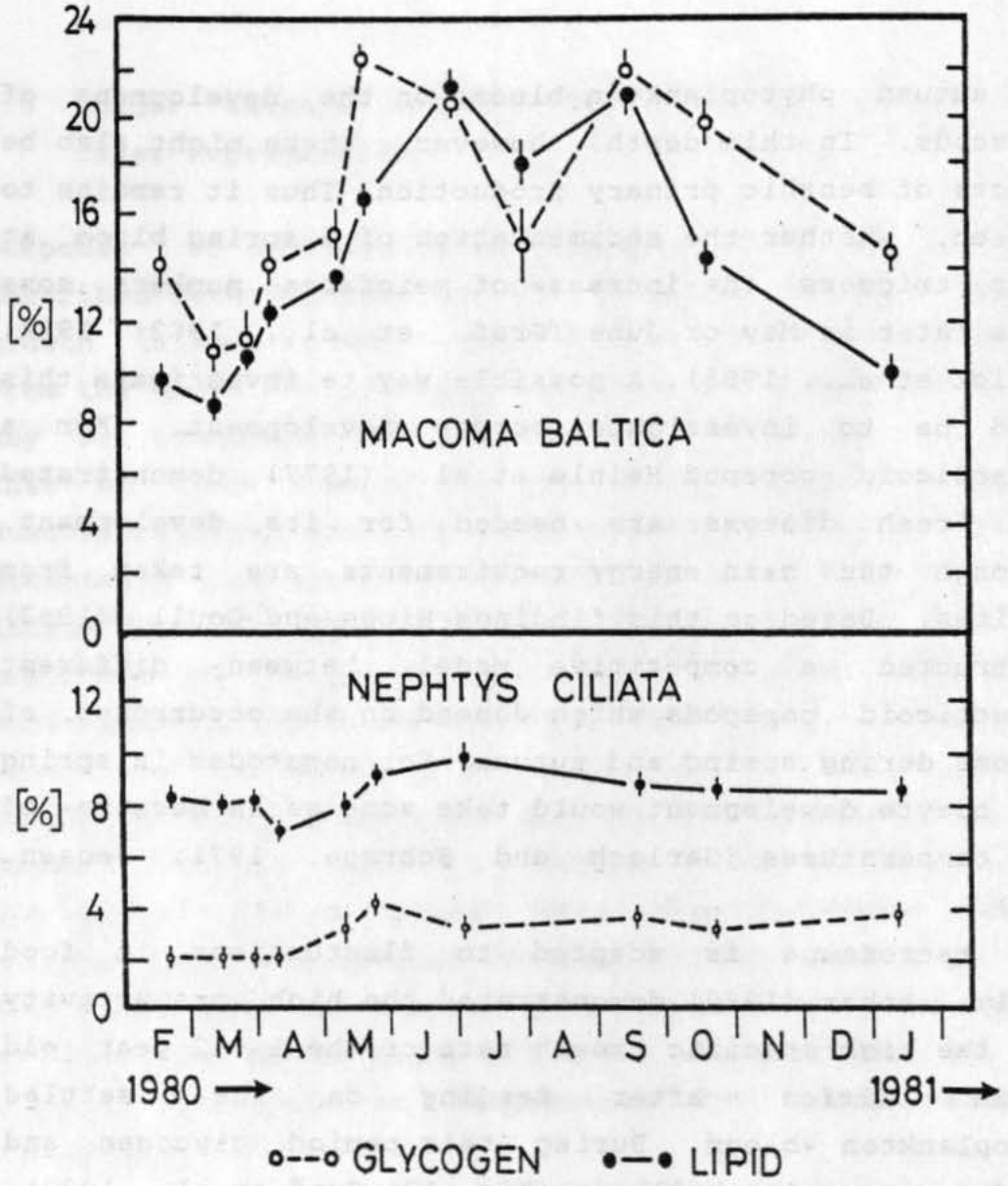

Fig. 13: Glycogen and lipid content of *Macoma baltica* and *Nephtys ciliata* from Boknis Eck (Western Kiel Bight) during 1981 . While *M. baltica* builds up glycogen and lipid reserves in late March concomitant with the settling spring phytoplankton bloom, this response was less evident and delayed for the predator *N. ciliata* (Redrawn after Graf et al., 1982).

2.4 Behavioral and physiological adaptations may increase the responses of the fauna.

After a bloom reaches the sediment surface a vertical migration of meiofauna starts, i.e,. animals from deeper sediment layers go to the sediment surface when it becomes attractive (Fig. 14; Schulz, 1983). In addition to food supply also an uplift of the chemocline (cf. 3.2) may also trigger the upward migration. Another possibility to exploit food at the sediment surface would be through enhanced bioturbation. An experiment to demonstrate this effect with *Pectinaria koreni* in microcosms, however, failed (Koeve and Graf, manuscript). *Pectinaria koreni* opens a funnel arround its tube when a bloom arrives at the sediment surface and thus the fresh material drops directly into its feeding cavity. This behavior even had the opposite result for the mixing rates of the sediment. However, this will not be a general finding.

Rice and Rhoads (1987) postulated for oligotrophic sediments that deep living infauna should pull food from the surface into the sediment to get rid of competition by vagile epifauna and by animals feeding in the sediment surface layer. This food collection should be especially pronounced, when food supply comes after a long starvation period. On the Vöring-Plateau (Norwegian Sea) at 1430 m water depth, about 500 sipunculans (*Nephasoma spec.)* inhabit about 10 000 burrows per square meter, so that each animal seems to have 20 vertical tubes. With their 6 mm long introvert they manage to cover 100% of the sediment surface (Romero-Wetzel, 1987). After a pellet pulse during spring the infauna, probably mainly sipunculans, pulled the settled food into the sediment. This process was depicted by a sudden increase of chlorophyll *a* concentrations down to 9 cm sediment depth

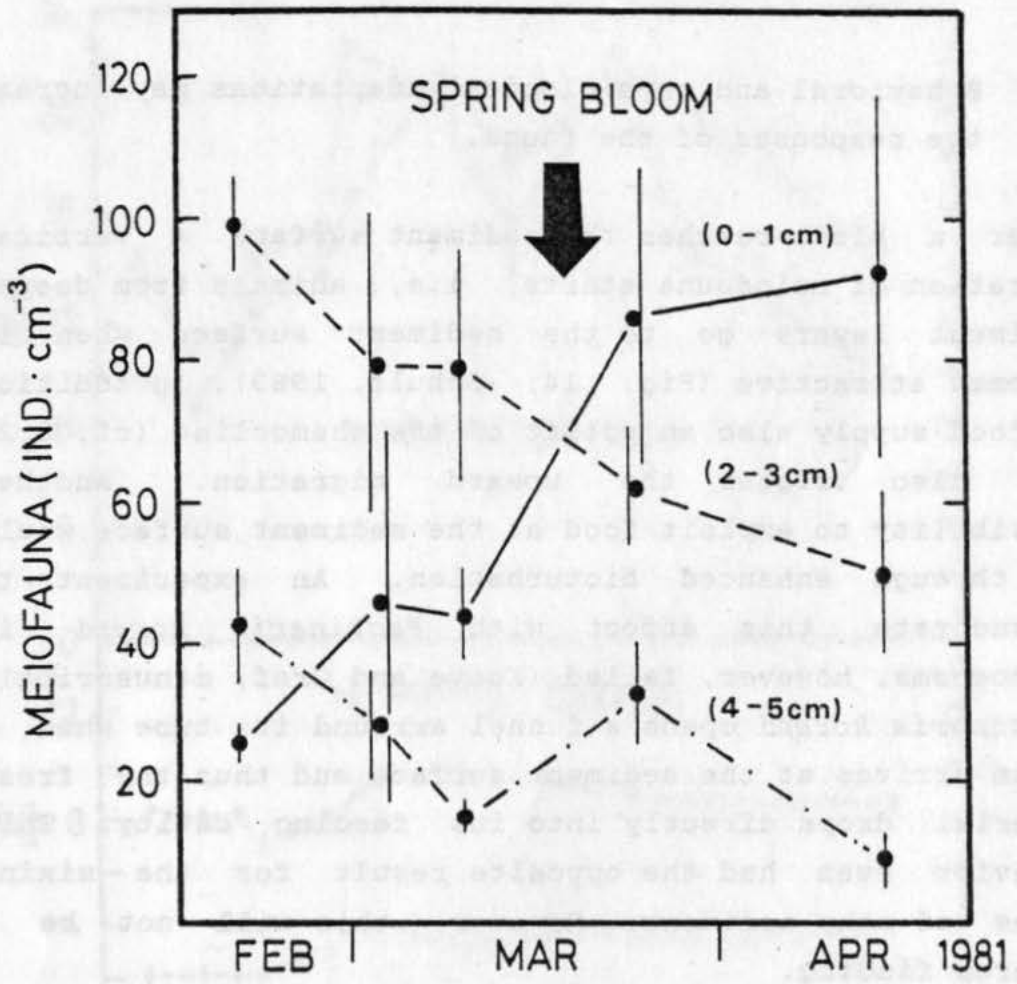

Fig. 14: After spring phytoplankton bloom sedimentation in mid-March 1981 meiofauna migrated to the sediment surface. (After Schulz, 1983).

within 8 days (Fig. 15; Graf, manuscript).
Scavenging macrofauna in the deep-sea have comparable problems with the fluctuations of their food supply. Smith and Baldwin (1982) demonstrated the physiological adaptation of *Paralicella caperesca.* This amphipod is able to enter dormancy with an extremly low respiration rate reducing energy losses during starvation periods.

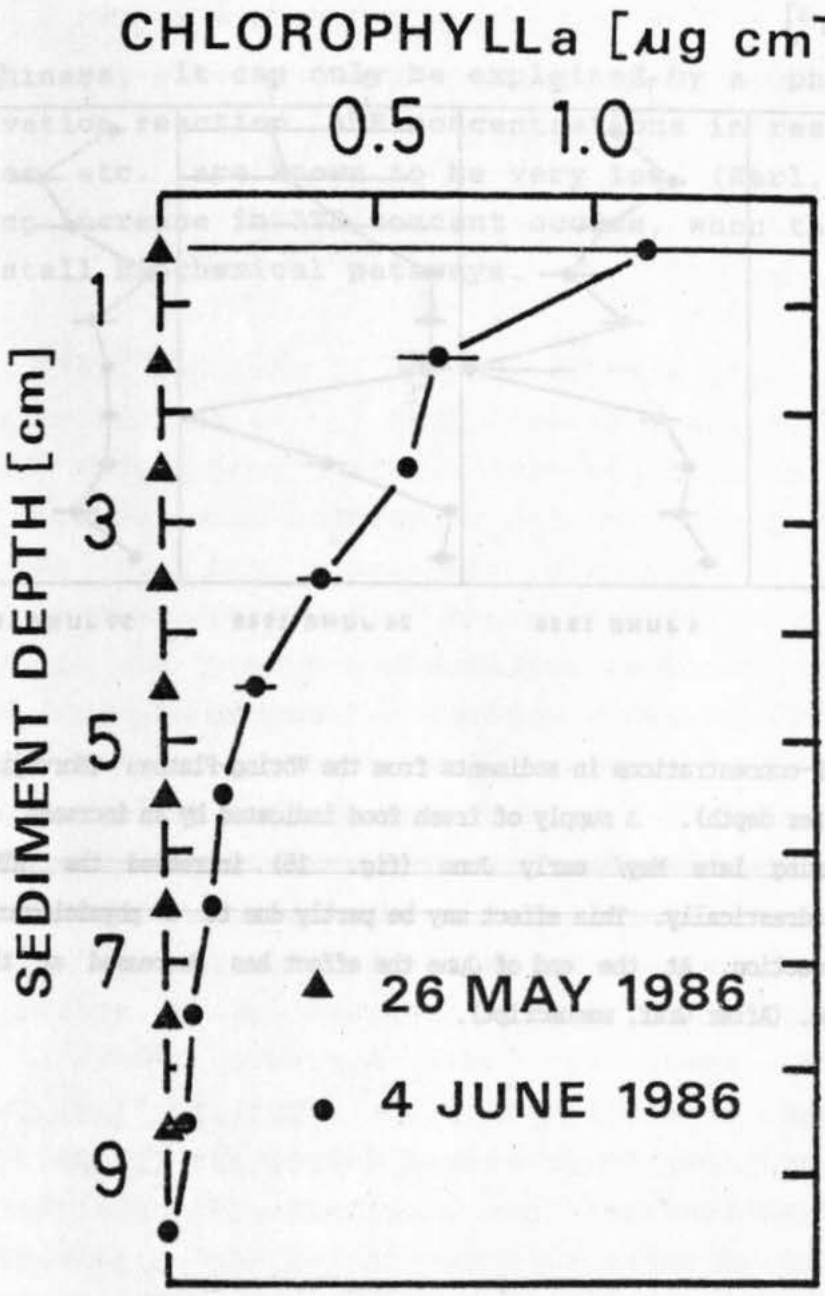

Fig. 15: Chlorophyll *a* in two sediment cores from the Vöring-Plateau (Norwegian Sea, 1430 m water depth); sampling interval of 1 week. A pellet pulse end of May increased the pigment content of the sediment by 3.3 µg cm^{-2} within a few days (After Graf, manuscript).

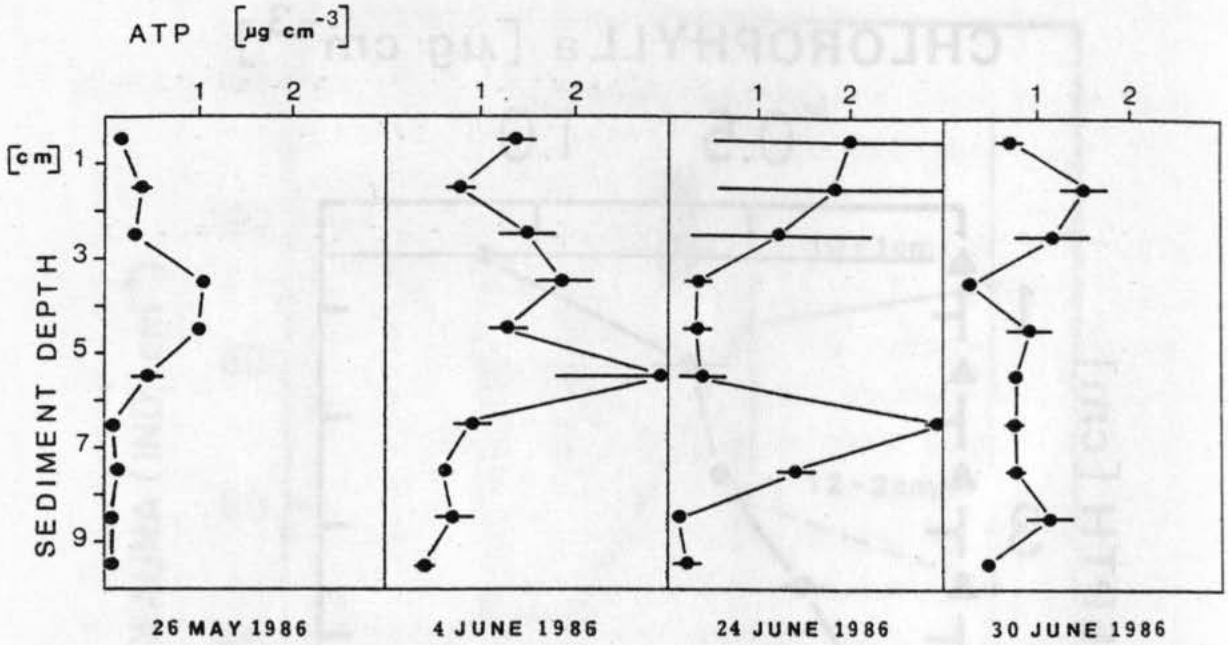

Fig. 16: ATP-concentrations in sediments from the Vöring-Plateau (Norwegian Sea, 1430 m water depth). A supply of fresh food indicated by an increase of chlorophyll during late May/ early June (fig. 15) increased the ATP-concentrations drastically. This effect may be partly due to a physiological reactivation reaction. At the end of June the effect has decreased at the sediment surface. (After Graf, manuscript).

However, as soon as the animals perceive the presence of a carcass or the bait in a trap, they awake immediately increasing respiration drastically. A first hint that such adaptations are more frequent in the deep sea, especially in the polar regions, where sedimentation is also extremely seasonal (Honjo et al.,1988), is depicted by the ATP response in the sediment from the Vöring-Plateau (Fig. 16; Graf, manuscript). The ATP-increase by a factor of 20 in the sediment surface cannot be explained by biomass increase alone. If it is not due to

patchiness, it can only be explained by a physiological activation reaction. ATP-concentrations in resting cells, spores etc. are known to be very low (Karl, 1980). A strong increase in ATP content occurs, when the organisms reinstall biochemical pathways.

3. The seasonal pattern of fluxes creates a non steady state.

3.1 Origin and quality of food supply follow distinct annual cycles.

The aim of models such as the one of Hargrave (1973, see fig. 1) or of Suess (1980), that try to correlate carbon flux to the sea floor with benthic respiration is to describe the global cycling of carbon. These authors were well aware of the short time scale and the seasonal pulses of particle flux but they assumed that such oscillations average out within one year or at least within several subsequent years. From a geological point of view or with respect to animals with long life spans this might hold true. However, smaller organisms with short life cycles depend on the actual food supply and not on a mean value.

In a boreal system the sedimentation pattern creates pulses of food supply to the benthos during spring and during autumn (Smetacek, 1980; Hargrave, 1980). In Kiel Bight as much as one third of the annual vertical input to the sediment may be delivered during such pulses; this creates an extreme seasonal imbalance. The analysis of these settling particles revealed that nutritional quality of this matter is much better than that of the mean settling particles. This could be shown by chlorophyll/carbon ratios for different coastal systems (Hargrave and Tagushi, 1978; Smetacek and Hendrikson, 1979; Skjoldal and Wassmann, 1986). The effects are strong enough to change C/N ratios in the nepheloid layer (for example from >10 to <6, Graf et al.,1982) and to create significant changes of OM concentrations in the sediment itself. Fig. 17 depicts the increase of chlorophyll *a* in the sediment after feeding a microcosm

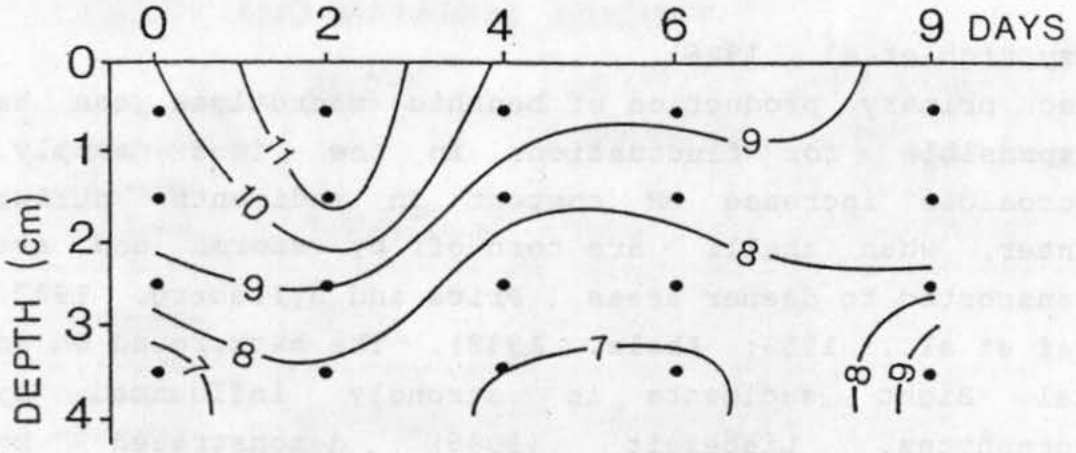

Fig. 17: Chlorophyll *a* isolines (µg cm^{-3}) in sediments from a microcosm experiment. After simulating a sedimentation event with cultivated diatoms on day 1, chlorophyll *a* increased significantly in the top 2 cm of the sediment. Although there is a high background level of chlorophyll *a* in the sediment due to natural autumn blooms and the added amount equals only half the quantity of a natural settling bloom, the event is clearly to be seen between day 1 and 4 (after Graf, 1987a).

with pelagic diatoms of carbon equivalent of 5.8 g C m^{-2}, which equals half the natural input during a spring or autumn bloom sedimentation event. Whether the input can be detected as an increase in OM content in the sediment itself, depends on the background content of OM. If lateral advection (LA) increases the food pulse significant changes in OM or protein are detected, even if the background is as high as 1% OM content, i.e. 130 g C m^{-2} in the 0-1 cm sediment slice of the corresponding station (Meyer-Reil, 1983). Also specific compounds of the settling material may change the chemical composition of the sediment. Because of its cellulose plates *Ceratium* in a settling autumn bloom changed the carbohydrate/protein ratios in the sediment of Kiel Bight

(Czytrich et al., 1986).
Also primary production of benthic macroalgae can be responsible for fluctuations in the food supply. Macroalgae increase OM content in sediments during winter, when thalli are torn off by storms and are transported to deeper areas (Price and Hylleberg, 1982; Graf et al., 1983; Abele, 1988). The background OM in Kiel Bight sediments is strongly influenced by macrophytes. Liebezeit (1986) demonstrated by carbohydrate analysis that 73% of this fraction in Kiel Bight sediments is derived from macrophytes. Even in the deep-sea of Lofoten Basin, Norwegian Sea, macrophytes are important (Liebezeit, pers. com.). The same was described for sediments from the Brainsfield Strait, Antarctica (Reichardt, 1987). However, a high background of macrophyte detritus does not indicate the actual importance of macrophytes, at least as long as the turnover of this matter is not known. During winter 1982 a response of the benthos to macrophyte input to the sediment of Kiel Bight was detected (cf. Fig. 9). Recently Abele (1988) depicted an input of red algae, which was as high as 125 g d.w. m^{-2} , or 30 g C m^{-2}, to a 17 m station in Kiel Bight, after one storm during summer. This event caused immediate anoxia at this station (Eversberg and Graf, unpublished data).
Benthic remineralisation was suggested to depend more on nitrogen supply than on carbon supply (Hargrave, 1980; Graf at al., 1983). Direct proof of this hypothesis was recently given by Kristensen and Blackburn (1987), who demonstrated that decay constants of PON are 2 - 3 times as high as for POC. Thus, the effect of bloom sedimentation as depicted in Fig. 5 is not only caused by the quantity of food supply but to a significant part is also due to the better quality, i.e the supply of nitrogen. This also explains the large effect of fresh

ENERGY AND MATERIAL BUDGET

	OXYGEN	HEAT	ORGANIC MATTER
		integrated over 7cm depth	
Consumption or production over 9 days	439 µg O_2 cm^{-2}	26.3 J cm^{-3}	1.3 LOSS 0.17 BLOOM 1.47 mg OM cm^{-3}
Assumption	RQ = 1	1 mg C = 40J	C : OM = 1 : 2
Carbon-equivalent	0.146 mg C cm^{-2}	0.66 mg C cm^{-3}	0.74 mg C cm^{-3}

Tab. 1: Comparison of a carbon budget via heat production and via oxygen consumption in a microcosm experiment simulating autumn bloom sedimentation (after Graf, 1987a).

material on the burning of old, rather refractory OM, as was demonstrated by Graf (1987a). In this study the input of 0.17 mg OM cm^{-3} from diatoms resulted in 1.3 mg OM cm^{-3} remineralization (cf. Tab. 1). The effect was called cooxidation.

Summarizing, it can be stated that food supply to the benthos creates a series of imbalances for the benthos. A conceptual model was constructed to demonstrate the different effects for the benthic community of a sublitoral station in Kiel Bight below the euphotic zone and without benthic primary production (Fig. 18, Graf, 1987 b). Benthic metabolism was split according to the origin of the food supply. Decomposition of stored, older material follows the annual temperature cycle and is influenced by the availability of oxygen (thin line, Fig. 18). Metabolism based on actual input of macrophytes (winter input) and an input of plankton spring and autumn blooms is indicated by the dashed line. When blooms

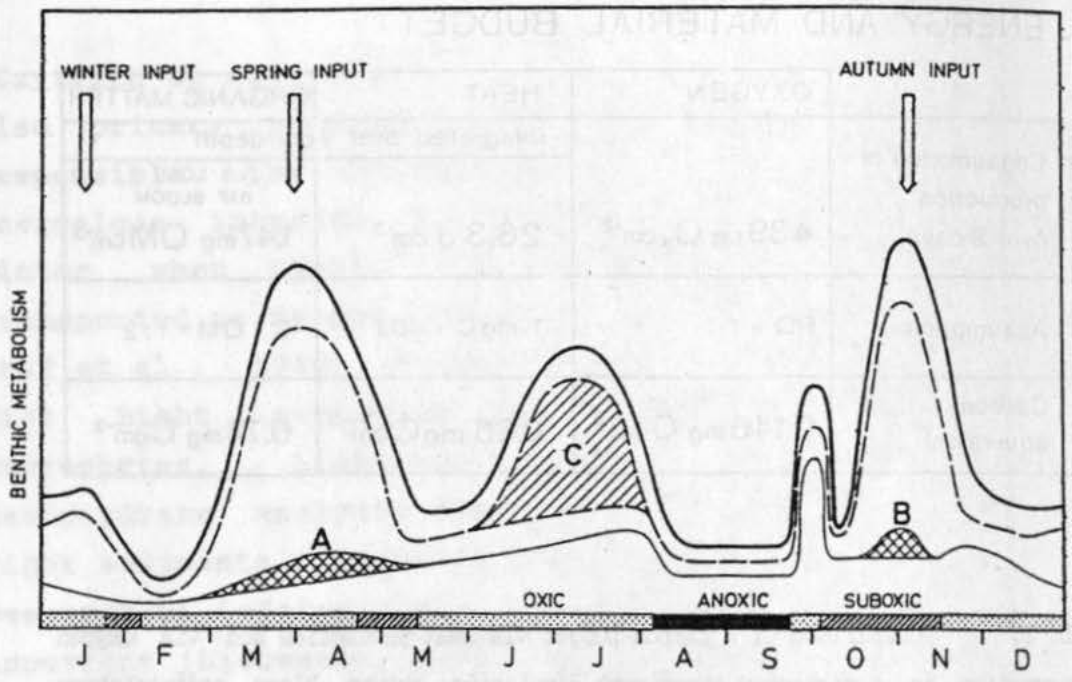

Fig. 18: Conceptual model for a sublitoral sediment station in Kiel Bight without benthic primary production. Total benthic metabolism is indicated by the solid line. The dashed line shows metabolism related to actual sedimentation rate. The thin line indicates metabolism based on stored organic matter in the sediment, which depends on temperature and on the availability of oxygen. Areas A and B depict cooxidation induced during bloom periods and area C depicts the influence of biodeposition by suspension feeding organisms in summer (after Graf, 1987b).

sediment, cooxidation (area A and B) has to be expected. Area C depicts the influence of biodeposition, which is especially pronounced during summer. The special problem of reduced metabolism during anoxia will be discussed later.

The model was based on field experiments until 1983. Since then additional events have been detected. During autumn we may find two blooms, whose fate is sedimentation (Noji et al., 1986). Also the break down of

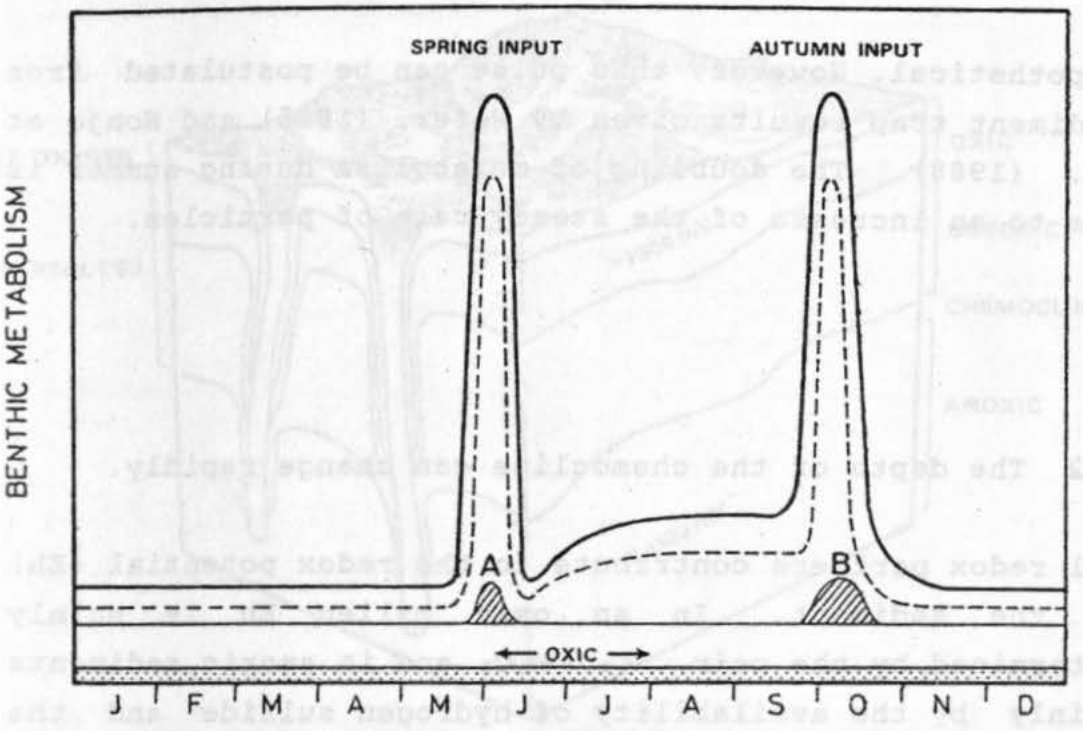

Fig. 19: Conceptual model for a 1400 m deep-sea station in the Norwegian Sea. The symbols are the same as in fig. 18. There is no change in temperature and in oxic conditions. According to observations described in figures 7, 15, and 16 there is some evidence for a response to spring input and to increasing summer sedimentation; the autumn peak is hypothetical and requires for confirmation.

a pelagic summer population caused by the first autumn storms can lead to a sedimentation signal. Decaying macroalgae may influence the sediment of Kiel Bight also during summer (Abele, 1988).

In the deep-sea there are less factors wich may lead to imbalances in food supply. A model may be constructed for the Vöring-Plateau sediments (Fig. 19). The shape of the curve for overall metabolism is much smoother during non bloom periods because temperature cycles and anoxia do not exist. Whereas there is some evidence for a response to food supply during spring (cf. Fig. 7, 15, 16) a second response to a food pulse during autumn is

hypothetical. However, this pulse can be postulated from sediment trap results given by Wefer, (1985) and Honjo et al. (1988). The doubling of metabolism during summer is due to an increase of the steady rain of particles.

3.2 The depth of the chemocline can change rapidly.

All redox partners contribute to the redox potential (Eh) in the sediment. In an oxic milieu Eh is mainly determined by the pair, O_2 / H_2O_2 and in anoxic sediments mainly by the availability of hydrogen sulfide and the pair, SO_4^{--}/H_2S (cf. Balzer et al., 1983 and literature cited therein). Other factors that influence Eh are the availability of electron acceptors such as O_2, NO_3^-, SO_4^{--}, and the organic matter in the sediment but also processes such as bioturbation by animals. Most of these factors were already mentioned in the RPD (Redox Potential Discontinuity)- layer concept of Fenchel and Riedl (1970). They divided the sediment into oxic, suboxic, and anoxic layers (Fig. 20). The bounderies were set to > 300 mV (oxic) and < 100mV (anoxic) (Jorgensen and Fenchel, 1974). The 100 mV boundery, also called the chemocline, depicts significant changes within a sediment profile: 1: below 100 mV free hydrogen sulfide occurs (Reimers, 1976), 2) this metabolite is toxic for animals, 3) it causes precipitation of many metals, and 4) pH is lowered (fig. 20).
The effect of bioirrigation via tubes is a later addition to the original concept (cf. Jorgensen and Revsbech, 1985; Meyers et al., 1987). There is only a thin layer where free oxygen is measurable with a microelectrode along the tube walls and at the sediment surface itself

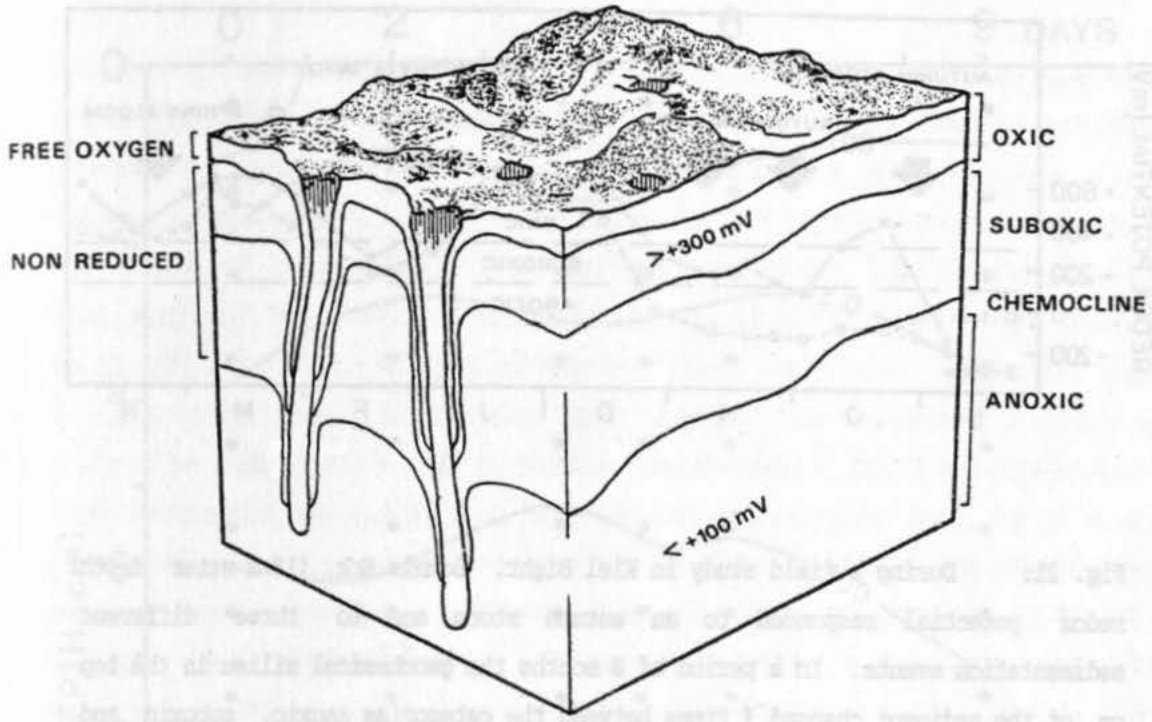

Fig. 20: The RPD (Redox Potential Discontinuity)-layer concept of Fenchel and Riedl (1970). The sediment is divided into anoxic, suboxic and oxic layers. Along the walls of tubes and burrows of animals the redox isolines are depressed (cf. Jorgensen and Revsbech, 1974). However, according to microelectrode measurements of oxygen, the so-called oxic layer does not really contain free oxygen over the entire depth.

(Revsbech et al., 1979). The latter finding is contradictory to the originally defined oxic layer, which was believed to depict free oxygen down to Eh > 300 mV. Thus there exists a "free oxygen layer" and a "non reduced layer"; the latter is comparable to the suboxic layer of the Fenchel and Riedl concept plus a part of the old oxic layer (fig. 20). In this non reduced layer there must be sufficient electron acceptors (for example NO_3^-) that are energetically more efficient than SO_4^{--} (cf. Sorensen et al., 1979), or sediment mixing and turbulence by bottom currents must be sufficient to periodically

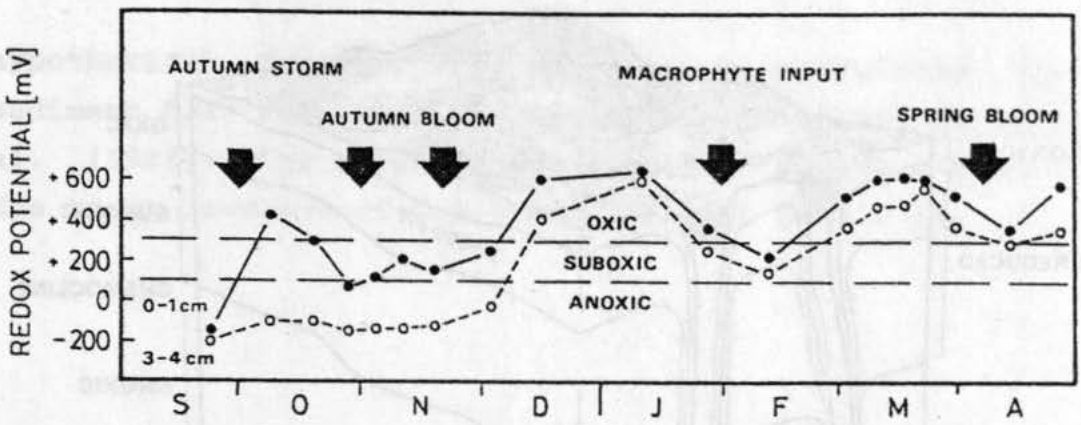

Fig. 21: During a field study in Kiel Bight, Boknis Eck, (18 m water depth) redox potential responded to an autumn storm and to three different sedimentation events. In a period of 8 months the geochemical milieu in the top cm of the sediment changed 7 times between the categories anoxic, suboxic and oxic (redrawn after Graf et al. 1983).

introduce oxygen to prevent the development of sulfate reducing bacteria.

Seasonal changes of the position of the chemocline have been described by Reimers (1976), and Jorgensen (1980). These authors demonstrate an uplift of the chemocline during summer. Fig. 21 (Graf et al., 1983) shows the immediate response of the chemocline position to an autumn storm, to several blooms, and to macrophyte detritus input in Kiel Bight.

In an experimental microcosm approach it could be shown that the chemocline may rise as fast as 1 cm within one day (Fig. 22) after introducing OM to the sediment. Thus, the observed pattern of food supply together with physical disturbances creates a pattern of geochemical changes in the sediment. One consequence of an uplift of the chemocline is increased nutrient release from the sediment. This holds true for inorganic nitrogen but

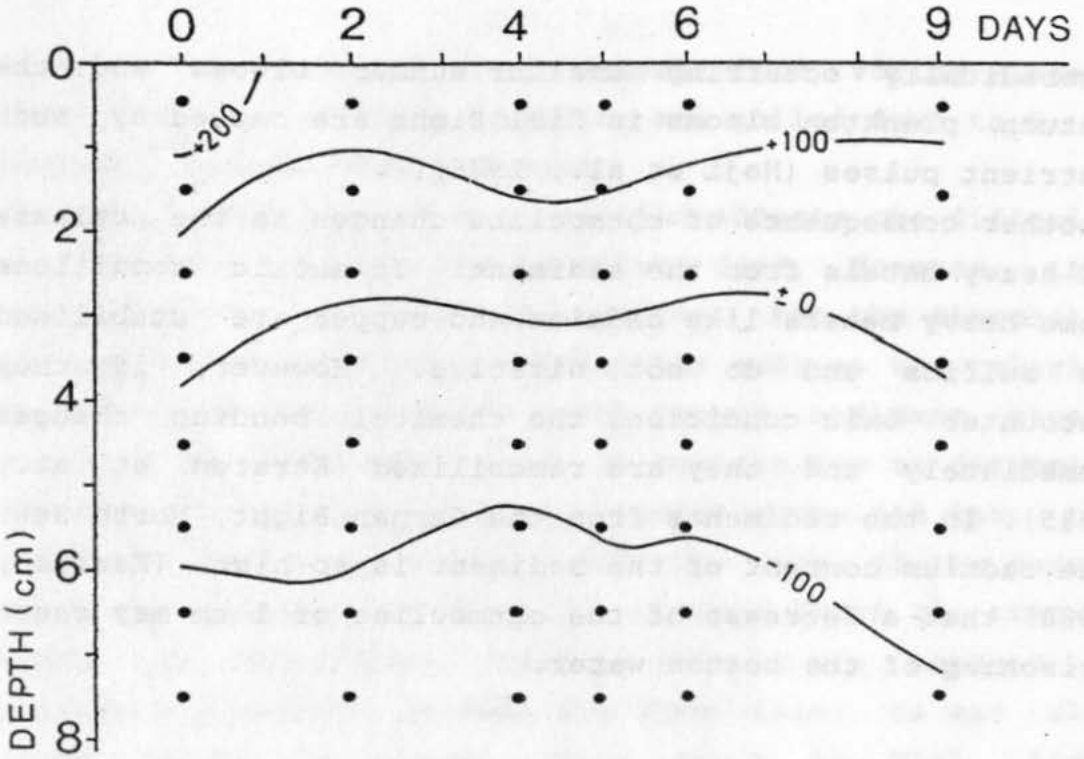

Fig. 22: Redox potential (mV) in sediments from a microcosm experiment. After feeding with fresh diatoms the chemocline (+100 mV) rose to 1 cm sediment depth within a day (after Graf, 1987a).

especially for phosphate, whose release from the sediment increased by a factor of 9 during the change from oxic to anoxic conditions in Kiel Bight (Balzer et al., 1983). A food pulse to the sediment thus creates an increase of nutrient release by two mechanisms: first by an increase of metabolism (cf, Kelly and Nixon, 1984) and second by a change of the geochemical milieu, which in return is influenced by metabolic reactions.

The nutrient pulses from the sediment are of interest for the annual development of the pelagic system. New production may start, if the pulses reach the euphotic zone (Smetacek and Pollehne, 1986; Pollehne, 1986). The

sporadically occurring smaller summer blooms and the autumn plankton blooms in Kiel Bight are caused by such nutrient pulses (Noji et al., 1986).
Another consequence of chemocline changes is the release of heavy metals from the sediment. In anoxic conditions some heavy metals like cadmium and cupper are stabilised as sulfids and do not dissolve. However, if they encounter oxic conditions the chemical bonding changes immediately and they are remobilized (Kersten et al., 1985). In the sediments from the German Bight, North Sea, the cadmium content of the sediment is so high (Kersten, 1988) that a decrease of the chemocline of 1 cm may cause poisoning of the bottom water.

3.3 Surface effects immediately influence deeper sediment strata

Benthic-pelagic coupling is by no means restricted to the sediment-water interface. During the spring bloom period Reimers (1976) observed increased hydrogen sulfide concentrations in 6-8 cm sediment depth, and Bengtsson (1982) reported increased heat production in 10 cm depth. In terms of ATP -biomass increase examples are given by Graf et al. (1983) and in Fig. 10. A food pulse to the sediment surface changes the whole sediment profile and induces exoenzymatic activity in deep sediment strata (Meyer-Reil, 1987b).
An explanation of the fast deep reaching response could be the fast particle and porewater transport by bioturbation. Mixing rates are summarized by Lee and Swartz (1980) and it turned out that fluid transport in the sediment is faster than particle reworking by a factor of 10. Nevertheless, also particle transport can

be fast, as is shown by the example from Vöring-Plateau (cf. fig. 15), where pellets are pulled down to 9 cm sediment depth within 8 days.
For the description of bioturbation effects the diffusion coefficient of Fick`s law is often used. However, this coefficient is not very illustrative. For the discussion of deep reaching effects a parameter such as the velocity at which surface effects reach deeper sediment strata seems to be preferable. Fig. 23 depicts how to determine the velocity of a particulate tracer entrained into the sediment (Mahaut and Graf, 1987).The slope of the curves gives the velocity at which for example 2% of the tracers reach the chemocline. When no animals are present to perform a transport through the chemocline, as was also found during an autumn field study in Kiel Bight (Czytrich et al., 1986), velocity of particle transport is significantly reduced and may be as small as 1 mm d^{-1}. Fluid transport is much faster. If only molecular diffusion is the driving force, i.e. no animals are present, a fluid tracer such as bromide reaches 4 cm sediment depth after 1 day and 8 cm after 4 days (Dicke, 1986; Kitlar, 1988). For bioirrigation this velocity has to be multiplied by up to a factor of 10, depending on the type of macrofauna included (cf. Lee and Swartz, 1980). However, because there is usually a strong gradient in fluid tracer distribution with depth, only few molecules actually reach the deeper strata. Nevertheless they can have drastic effects. Firstly, they may provide a signal or trigger inducing the upward migration of animals to the surface or the enhancement of the pumping of water through burrows. Secondly, metabolic activity may be stimulated, if the molecules are essential for metabolism. The latter will hold true for nitrogen containing molecules such as amino acids (cf. 3.1). The enrichment of fresh organic matter at the

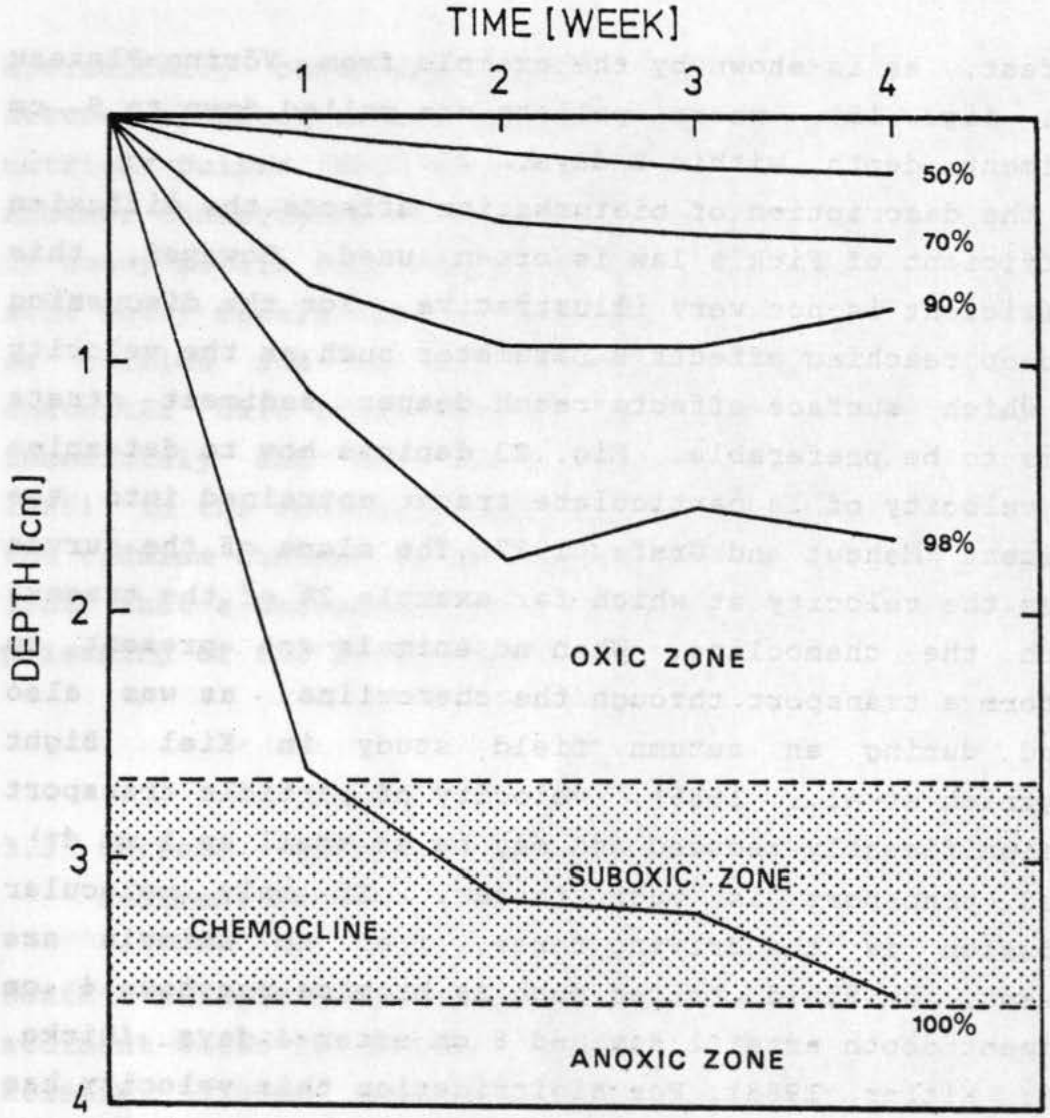

Fig. 23: Particulate tracer (luminophore) transport in experiments with natural sediment cores from Kiel Bight. The curves give the depths to which 50, 70, 90, 98 and 100% of recovered luminophores are distributed within a period of up to 4 weeks. From the slopes of the curves a bioturbation velocity can be calculated. For example, 2 % = 100% - 98% of the introduced tracers reached the chemocline (about 3.5 cm) within 1 week, i.e. at a velocity of about 5mm per day (redrawn after Mahaut and Graf, 1987).

sediment surface observed after spring bloom sedimentation will cause increased amino acid concentrations at the sediment surface, especially when the fragile plankton cells are disrupted and start to leach. For this reason, Koeve and Graf (manuscript) measured total amino acids during a spring bloom simulation experiment (Fig. 24). While the unfed controls showed stable amino acid concentrations, in the cores enriched with algae amino acids increased dramatically, particularly immediately above chemocline. Even in the deepest layers analysed (10-11 cm) amino acid concentration doubled within 7 days.

The deep reaching effect of the above experiment was also achieved by a combination of particle transport and fluid transport. Particle tracers demonstrated that the bloom was mixed down to the chemocline (3 cm sediment depth) within two days (cf. fig. 25). In this layer the most efficient conversion of POC into DOC occurred as is depicted by the increase of amino acid concentration up to > 300 µmole dm^{-3} (Fig. 24). From this extreme concentration an effective diffusion flux is generated, which transports amino acids to deeper sediment strata. Thus, the combined effects of particle and fluid bioturbation can easily explain the observed deep reaching effects. The above cited field observations of extreme changes of whole sediment profiles agree with simulation experiments in the laboratory.

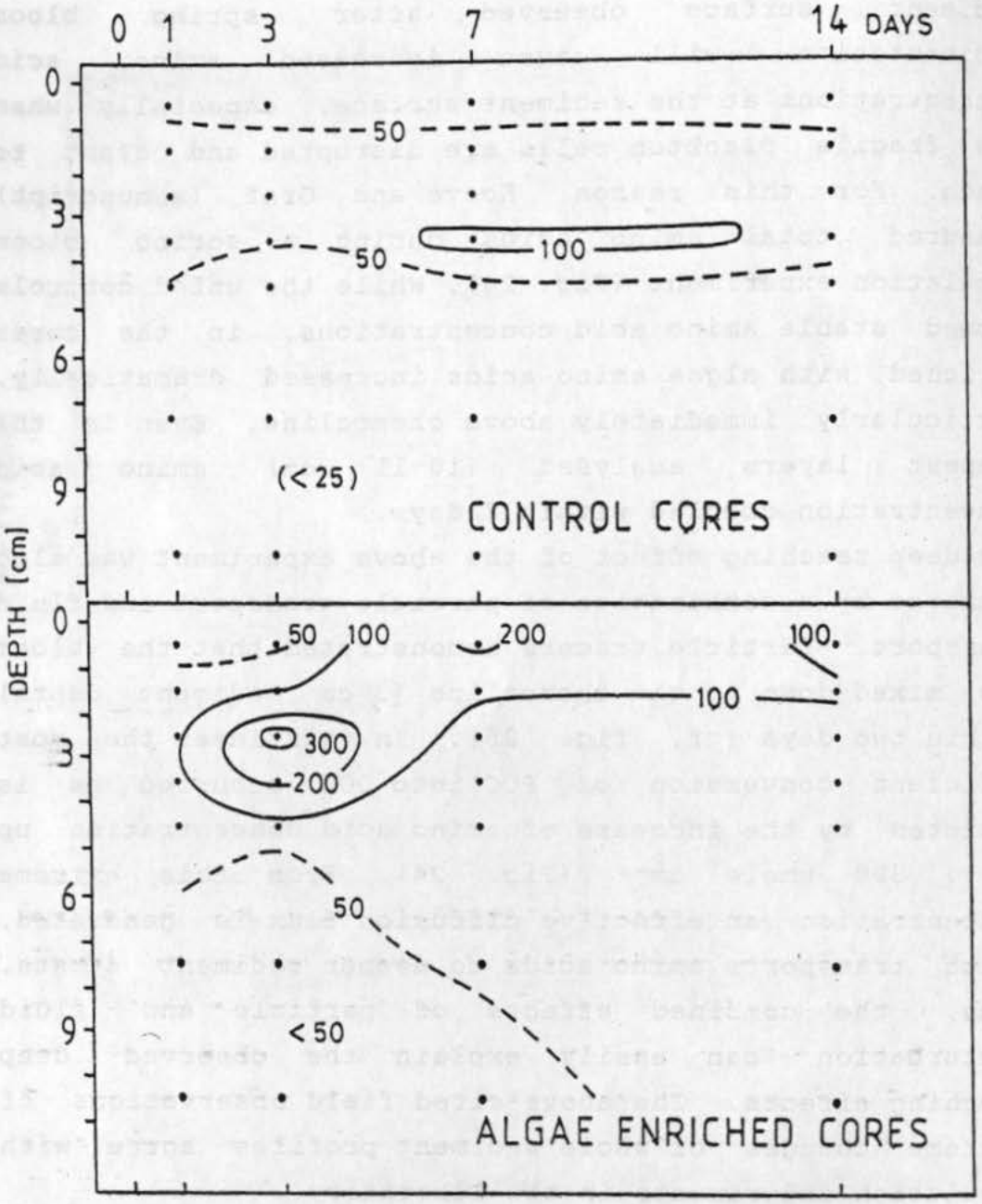

Fig. 24: Development of total amino acid concentration (o-Phthalaldehyde - Reactive - Substances (ORS) given in µmol glycine-equivalent dm^{-3}) in the porewater of microcosms. In the control cores concentrations stay constant with a maximum at the chemocline at about 3 cm sediment depth. After feeding on day 1 an extreme concentration developed at the chemocline. Via diffusion and bioirrigation this peak influenced surface layers as well as the deepest analysed sediment strata on day 7 (after Koeve and Graf, manuscript).

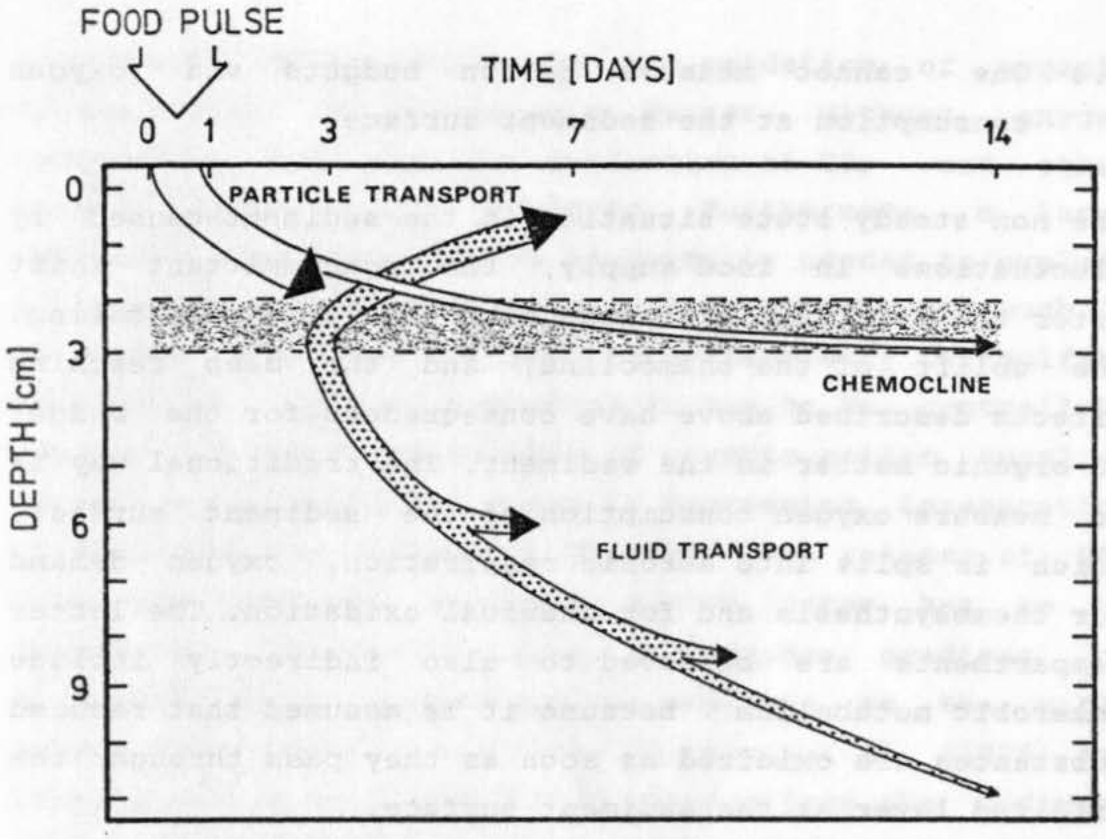

Fig. 25: Schematic graph of the combined effects of particle and fluid transport in an experiment simulating spring bloom sedimentation (cf. fig.24). Particulate food is transported down to 2-3 cm sediment depth within 2-3 days, is converted into dissolved organic matter near the chemocline and then distributed throughout the entire core. The extreme differences from the concentrations near the chemocline to deeper sediment strata create strong diffusion fluxes. For particles the chemocline may act as a barrier if no animals are present to achieve this transport (after Koeve and Graf, manuscript).

3.4 One cannot measure carbon budgets via oxygen consumption at the sediment surface

The non steady state situation in the sediment caused by fluctuations in food supply, the concommittant shift after the food supply towards more anaerobic metabolism, the uplift of the chemocline, and the deep reaching effects described above have consequences for the budget of organic matter in the sediment. The traditional way is to measure oxygen consumption of the sediment surface, which is split into aerobic respiration, oxygen demand for chemosynthesis and for chemical oxidation. The latter compartments are believed to also indirectly include anaerobic metabolism, because it is assumed that reduced substances are oxidized as soon as they pass through the oxidized layer at the sediment surface.

The comparison of an oxygen budget versus a heat production budget in the sediment results in extreme discrepancies (Graf, 1987a). Oxygen explaines only 3% of the carbon losses during 9 days (Tab. 1). This amount is equivalent to the carbon equivalent of oxygen consumption in the few mm thin free oxygen layer of the sediment, whereas heat production accounts for 89% of the lost carbon integrated over 7 cm sediment depth.

Several reasons explain the discrepancies. Starting with methodological problems oxygen consumption may be underestimated because of new production of oxygen from hydrogen peroxide via catalase activity (Pamatmat, 1988). Second, fermentation processes do not occur in the geochemical oxidation model. They are the main reasons for discrepancies in oxygen versus carbon dioxide budgets, which have been reported by Pamatmat (1968), Hargrave and Phillips (1981) and Grant and Hargrave (1987). Hanson and Tenore (1981) demonstrated that the CO_2 : O_2 ratio can be 50 : 1 when macrophyte debris is

decomposed. Fermentation is the oxidation of organic matter with other organic matter without oxygen consumption but with the production of CO_2 and other organic matter as end products. Furthermore, a large consumption of fermentation products is needed to explain sulfate respiration. Up to now it is unknown how much OM is needed to produce the substrates necessary for sulfate respiration. In future studies it has to be controlled, whether an increased quality of organic matter supplied during a sedimentation event is increasing fermentation processes in the sediment. Thirdly, the release of DOC from the sediment into near bottom water has to be considered especially when an extreme gradient of dissolved amino acids from the sediment to the water exists (fig. 24). In studies of Nixon et al. (1976) and Christensen et al. (1983) DON release from the sediment explained a major part of the carbon budget, a finding that also suggests that the DOC pool in the water column is strongly influenced from the sediment.

In the deep-sea of the Vöring-Plateau, Norwegian Sea, where free oxygen penetrates several centimeters deep into the sediment Forster and Graf (unpublished data) found nearly equivalent carbon budgets 1) via O_2-consumption in the overlying water, 2) via O_2-microprofiles and 3) via heat production. Experiments were conducted during summer when the presence of a steady state system can be assumed (cf. fig. 19). In shallow coastal waters, however, carbon budgets via heat production and via oxygen consumption must be different, especially during periods of non steady state.

For carbon budgets established just via oxygen consumption of the seabed this means that the final oxidation of reduced substances must also be considered in the water column above the sediment, including lateral and vertical exchange mechanisms (cf. Boynton et al.,

1980). In Kiel Bight O_2-consumption in the several meters of the subpycnocline water column is on the same order of magnitude as the consumption at the sea floor (Babenerd, 1988). To summarize it can be stated that the problems of short time scales of benthic-pelagic coupling with its sequences of non steady state situations should be included in the OM flux models mentioned in the introduction. The changes towards anaerobiosis and fermentation provide effluxes from the sediment which are not counterbalanced in an annual mean value. This means that the real carbon flow through the sediment is underestimated.

4. Processes in the near-bottom layer provide the key to realistic budgets of the carbon cycle.

4.1 Biodeposition and lateral advection dominate over vertical sedimentation

A theoretical comparison of extremely high sinking velocities of 200 m d^{-1} = 0.23 cm s^{-1} with very low current velocities of 2 cm s^{-1} depicts that for a benthic organism the benthic-pelagic coupling is more a horizontal than a vertical event. This is true even during the sedimentation of a plankton bloom.
Particle concentration in the water above the sea floor is increased by resuspension and by changes in sinking velocity. Benthic animals themself contribute to the maintenance of elevated levels by bioentrainment (BE) and by tubes reaching into the water column, which increase turbulence (Carey, 1983, Eckmann, 1985). In near-coastal areas such as Long Island Sound (USA) this near-bottom layer was called the benthic turbidity zone (BTZ) covering the lower 6-9 m of the water column (Rhoads et al., 1984). In the deep-sea this zone was called nepheloid layer and may be as thick as several hundred meters (cf. Gardner et al., 1985).
In Kiel Bight particle content of bottom water (seston concentration) is about 3 mg l^{-1} and much higher during bloom periods or during storms (Kolmel, 1977). If we assume 1) 1 mg OM l^{-} for the organic fraction, 2) a current velocity of 2 cm s^{-1} and 3) that suspension feeders may influence a 5 cm water layer above the sediment, it can be calculated that 32.5 kg available OM yr^{-1} reaches a model square meter of seafloor (cf. Muschenheim, 1987a,b). The latter estimate must be regarded as conservative. This simple approximation depicts that OM should not be limiting to benthic

organisms, if they are able to collect particles out of the water and provided this OM is at least partly digestible. Experiments on macrofauna colonization and succession in sterile sediment of the "Hausgarten" area in Kiel Bight resulted in an extreme increase of abundance and biomass compared with the natural sea floor (Arntz and Rumohr, 1982). The experimental set up was elevated over the sea floor, providing an advantage for suspension feeders. Biomass values increased up to 1 kg w.w. m^{-2} within 1 year. It is obvious that food consumption of organisms in the artificial sediments must have been in the range of several kg OM $m^{-2}yr^{-1}$.

Also in the natural benthic community suspension feeding is an important process, as can be estimated by production rates of suspension feeders. In Kiel Bight an example is given by Brey (1984), who estimated the production of *Mya arenaria* to be about 15 g C $m^{-2}yr^{-1}$. Assuming a P/C ratio of 15 % this means a food consumption of 100 g C m^{-2} yr^{-1}. Vertical sedimentation, which is 40 - 60 g C $m^{-2}yr^{-1}$ (Smetacek, 1980) cannot even explain the production of this one macrofauna species. In shallow water the effect of suspension feeders may be strong enough to control phytoplankton growth (Officer et al., 1982). In the euphotic zone of Kiel Bight production of such benthic suspension feeders is no problem for carbon budgets, because the remineralized food starts regenerated production. Below the pycnocline, however, in the aphotic zone, where the above mentioned colonization experiments were carried out, carbon budgets cannot be explained by vertical sedimentation alone.

Suspension feeders are also important for other benthic organisms. Depending on their way of defecation they increase the OM content in the sediment, a process called biodeposition (BD), or they reject pellets into the benthic turbidity zone, which is termed bioentrainment

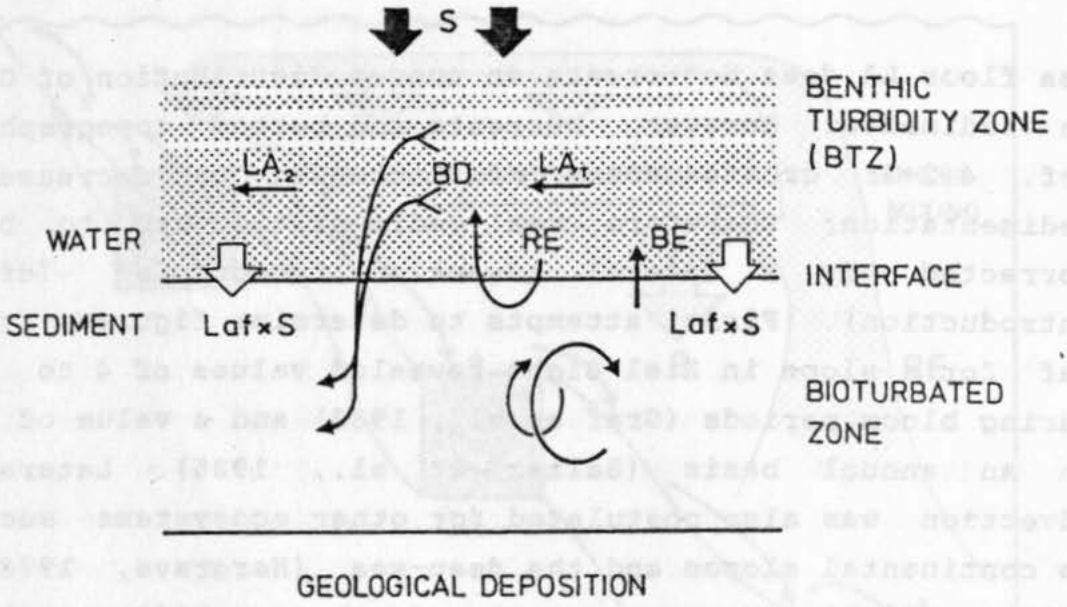

Fig. 26 Scheme of processes that determine the POC content of the benthic turbidity zone (BTZ). S = sedimentation, LA = lateral advection, BD = biodeposition, RE = resuspension and BE = bioentrainment.

(BE). After spring bloom sedimentation the spionid *Polydora ciliata* in Kiel Bight increased the amount of food supply for other organisms by a factor of 2. This was achieved by suspension feeding and subsequent deposition of pellets and as well as by the additional trapping effect of the tubes themself. Chlorophyll *a* concentrations in the sediment were twice as high as in sediments without Polydora. Such food enrichment provided an exellent habitat for meiofauna and foraminifera, which increased their abundance down to several cm sediment depth (Schmager, 1988).

Fig. 26 summarizes the processes relevant for the POC content in the benthic turbidity zone. The POC pool within this zone is fueled by sedimentation (S), by resuspension (RE) and by bioentrainment (BE). At a level

sea floor LA does not create an uneven distribution of OM in sediments. However, currents and bottom topography (cf. 4.2+3) create areas of increased or decreased sedimentation; therefore real sedimentation has to be corrected by a lateral advection factor Laf (cf. introduction). First attempts to determine figures for Laf for a slope in Kiel Bight revealed values of 4 to 7 during bloom periods (Graf et al., 1983) and a value of 2 on an annual basis (Balzer et al., 1986). Lateral advection was also postulated for other ecosystems such as continental slopes and the deep-sea (Hargrave, 1978, Smith, 1987). However, most of these studies only compared sediment trap results with benthic activity. From the discussion on biodeposition it becomes obvious that Laf was not estimated, but rather a mixture of effects from LA and BD.

4.2 Refractory material is kept for many years in a resuspension loop.

The organic part of freshly produced phytoplankton is almost completely burned in the sediment as demonstrated before. Even carotinoids, which were believed to be especially stable, are significantly reduced in an oxic environment (Abele, 1988). The high background level of OM in the sediment comes from structural components of macrophytes (cf. Liebezeit, 1986), from terrestrial input and from fossil carbon, which is supplied by cliff erosion and by reworking of old material in the shallow areas (cf. Fig. 27). The latter two types of input were estimated to be 30 g C m^{-2} yr^{-1} in the deposition areas

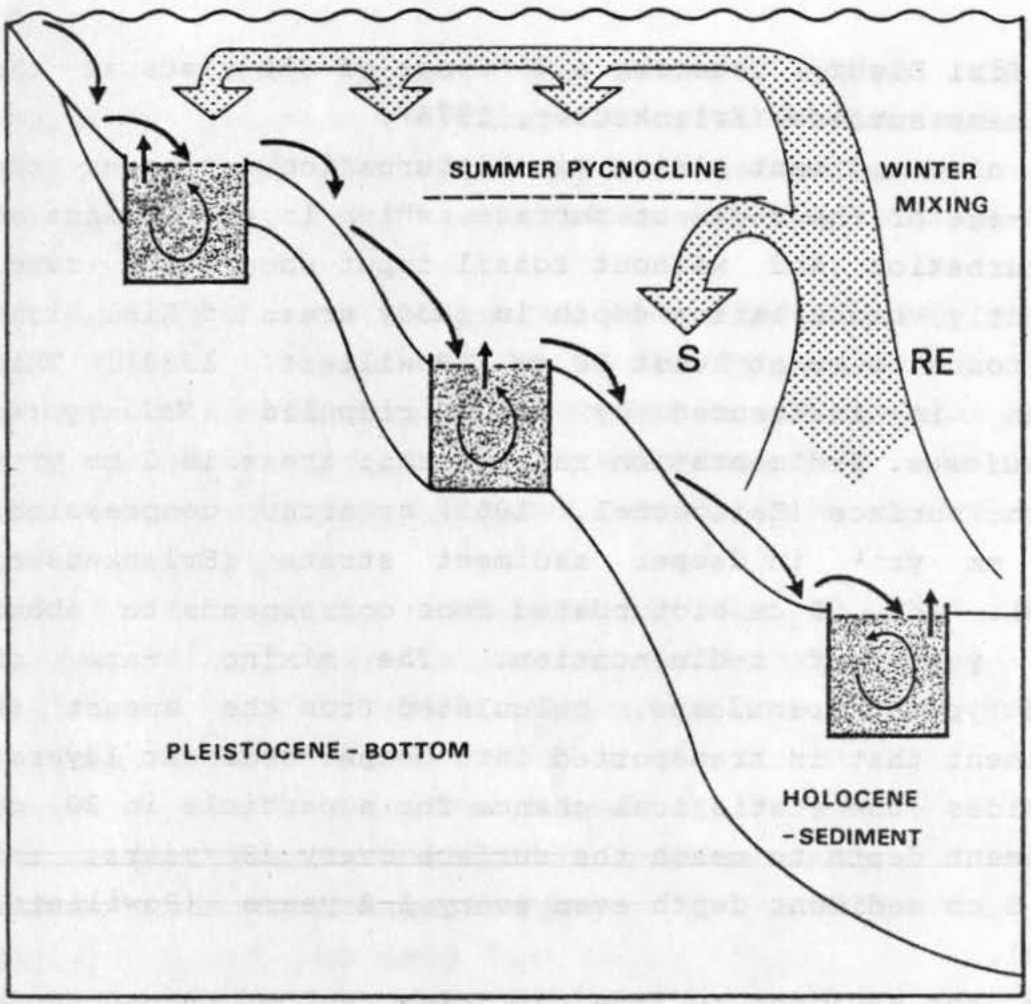

Fig. 27 Resuspension loop in the Kiel Bight channel system. During summer resuspension (RE) and resulting sedimentation (S) is only significant below pycnocline, whereas during winter a redistribution back to shallow areas also occurs. In shallow water bioturbation effects introduce pleistocene sediments to this loop and even in the deepest part of the channel particles have a statistical chance to be recycled for 140 years.

of Kiel Bight, creating a $\delta^{14}C$-age of 850 years at the sediment surface (Erlenkeuser, 1976).

But also sediment mixing via bioturbation increases the $\delta^{14}C$-age of the sediment surface, which in the absence of bioturbation and without fossil input should be zero. Recently, bioturbation depth in muddy areas of Kiel Bight was found to be at least 20 cm (Powilleit, 1988). This depth is influenced by the priapulid *Halicryptus spinulosus*. Sedimentation rate in this areas is 2 mm yr^{-1} at the surface (Zeitzschel, 1965) or after compression, 1.4 mm yr^{-1} in deeper sediment strata (Erlenkeuser, 1976). The 20 cm bioturbated zone corresponds to about 140 years of sedimentation. The mixing rate of *Halicryptus spinulosus*, calculated from the amount of sediment that is transported into deeper sediment layers, provides the statistical chance for a particle in 20 cm sediment depth to reach the surface every 38 years, and in 5 cm sediment depth even every 1-2 years (Powilleit, 1988).

From the sediment surface particles can be resuspended. During the turbulent winter season they may be redistributed over the whole area of Kiel Bight (Fig. 27). On their way through the water column they are chemically changed, for example the content of humic acids decreases (Hendrikson and Smetacek, 1979). After a storm during spring 1980 more than 300 g m^{-2} seston were found in a 20 m water column (Peinert et al., 1982) depicting how the pool of OM can be refilled in shallow areas. By measurement of OM and protein in the sediment this effect could be directly analysed (Graf et al., 1984, Meyer-Reil, 1983). For Chesapeake Bay (USA) great seasonal differences of OM content in the sediments have also been reported (Boynton and Kemp, 1982).

Fig. 27 shows that in Kiel Bight geological deposition, i.e. deposition below the bioturbated zone can only occur

in the deepest part of the channel system. In the shallower parts a reworking of pleistocene sediments occurs, whereas at medium depths holocene matter in a transitory way only accumulates to the bioturbation depth.

If no storms occur during the stratified summer period the lateral transport of OM in the subpycnocline water masses is less related to processes in the euphotic zone. Only some near-bottom lateral advection down the slope and small sedimentation rates contribute to the pool of OM in the sediment.

Before a particle statistically reaches geological deposition it has to survive many such resuspension loops including very different chemical milieus and enzymatic attacks. Nevertheless, even a recent particle has a chance to reach geological deposition in one step, if it is buried by bioturbation. This seems to be the major reason that a geological record of unchanged pelagic signals in the sediments does indeed exist.

Below bioturbation depth transport processes are not yet over. For a mineral particle diagenesis may cause dissolution and for particulate OM microbial degradation still continues. A carbon atom still has the chance to come back for example as methane, to be oxidized to carbon dioxide, to be heterotrophically fixed and to start the whole cycle again.

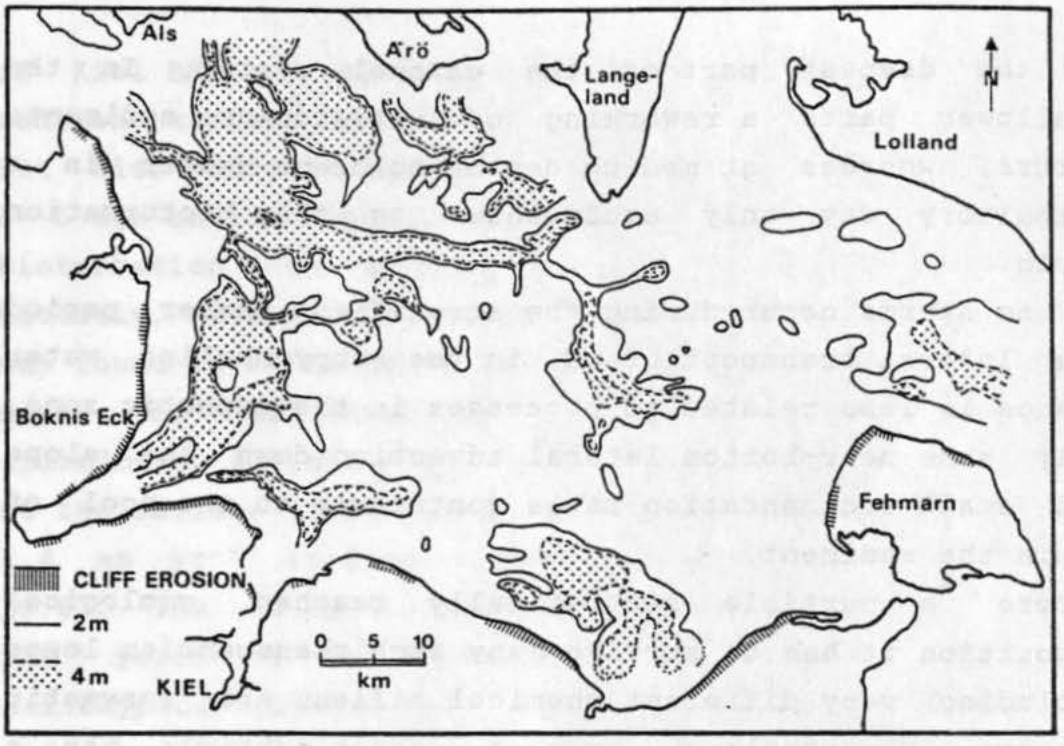

Fig. 28 Pachymetric map of Kiel Bight redrawn after Healy and Werner (1987). Areas with more than 4 m sediment are shaded. Comparing this map with Fig. 29 it becomes obvious that the sediments are mainly deposited in the channels.

4.3 Processes in the near-bottom layer create different types of sediment.

The final result of the long lasting lateral carbon and mineral transport is depicted by Fig. 28, which gives the pachymetric map of Kiel Bight, i.e. the sediment thickness. The post glacial marine sediments which accumulated in about 8000 years are deposited only in certain areas, which represent less than one half of Kiel

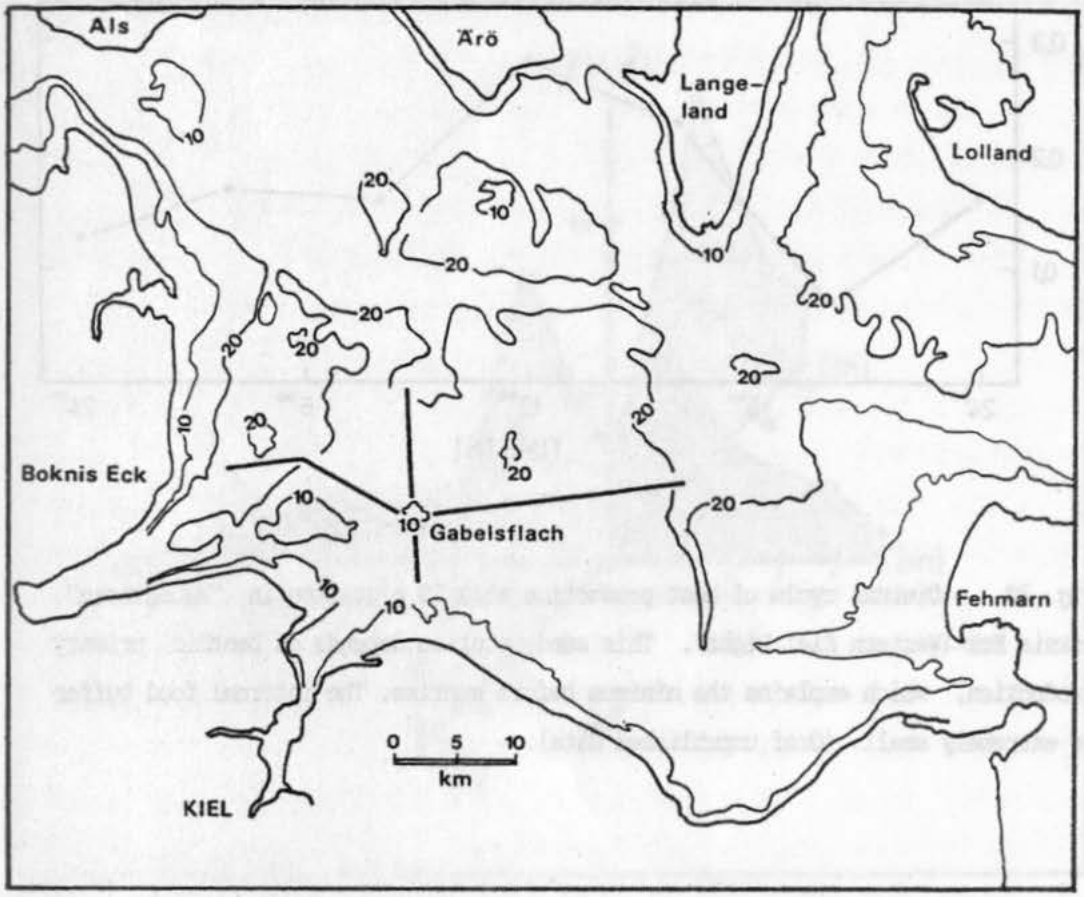

Fig. 29 Bathymetric map of Kiel Bight redrawn after Seybold et al., 1971, including the profiles of fig 31.

Bight. The thickest layers are found in the deepest channels (cf. Fig. 29), where they reach more than 10 m. The high content of OM, or food resource in these sediments, causes insufficient oxygen supply during the stratified summer period, with sometimes catastrophic consequences for the inhabiting fauna (Weigelt, 1987). In the shallow sandy areas of Kiel Bight erosion prevents a higher accumulation of OM. During spring and early summer a 10 m station lost about 375 g C m^{-2} to deeper areas (Graf et al., 1984). In these areas small organisms such as bacteria, protozoans and meiofauna depend on the suspension feeders, on organic matter deposited for short

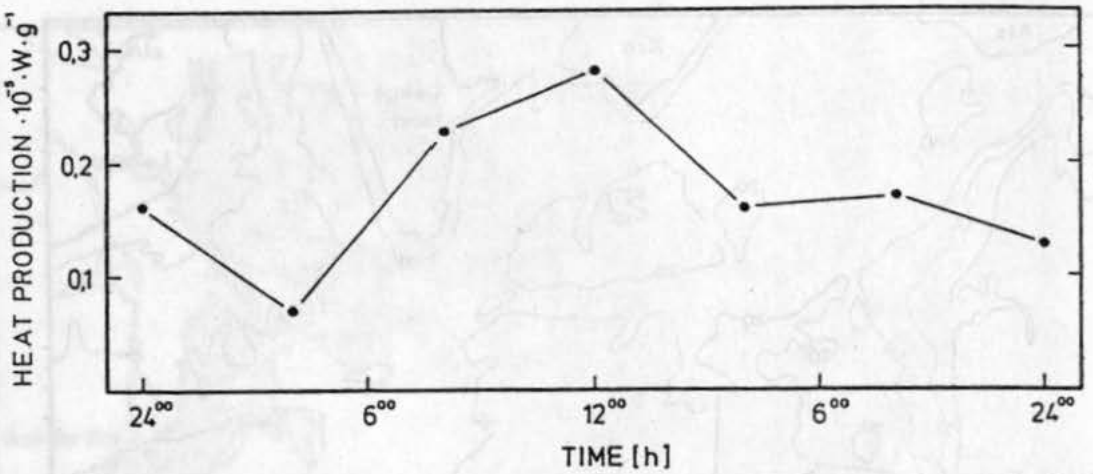

Fig. 30 Diurnal cycle of heat production at a 10 m station in "Hausgarten", Boknis Eck (Western Kiel Bight). This sandy station depends on benthic primary production, which explains the minimum before sunrise. The internal food buffer is extremely small. (Graf unpublished data).

periods on the surface, and on benthic primary production. Benthic diatoms cause a diurnal cycle in activity of small organisms, with low values at the end of the night (Fig. 30). Similar results were reported by Faubel and Meyer-Reil (1983) based on enzymatic measurements of isolated fauna, indicating that no food reservoir is available and that activity breaks down as soon as the daily benthic primary production is consumed.

For benthic meio- and macrofauna optimal habitats in Kiel Bight are at a depth range of 17 - 20 m (Scheibel, 1976; Arntz, 1978). This range combines good food supply with acceptable oxygen supply. Fig. 31 depicts that in these areas most organic matter is burned. On 4 profiles from a 10 m central flat (Gabelsflach) towards the surrounding channel system heat production and OM content of the top 4 cm of the sediment was analysed in June 1987. The

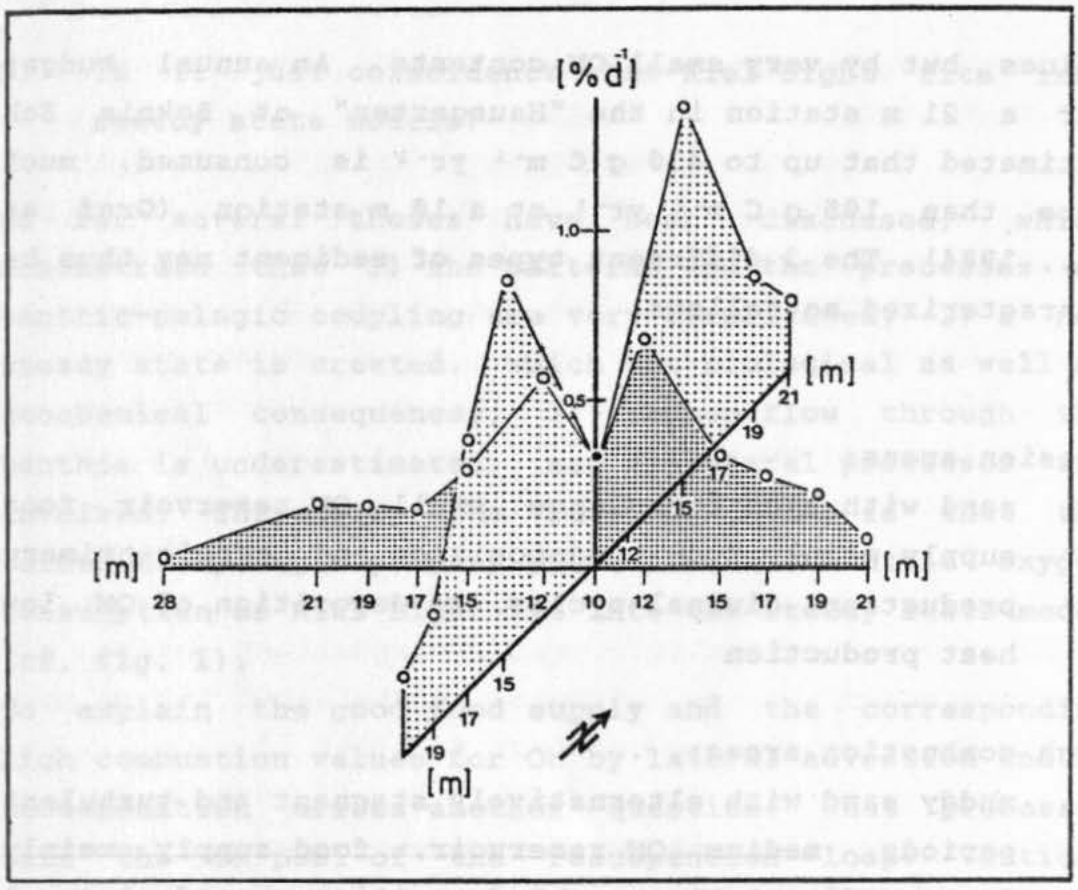

Fig. 31 The ratio heat production versus organic matter content of the sediment (0-4 cm) expressed as % d^{-1}. 1% d^{-1} means that the sediment can live 100 days from the standing stock assuming the measured heat release. In the deepest part of the channels (28 m) the stock would last for years, if it would be possible to burn it.

figure depicts the ratio of heat production versus OM as % per day i.e., how much of the stored OM is burned per day. In the high combustion areas the stored OM is sufficient for about 100 days of heat production if all OM is digestible. In the deepest parts, however, OM is enough for several years. The ratio of heat production versus OM is especially high in the 12 - 15 m range. This ratio, however, is not created by high heat production

values but by very small OM contents. An annual budget for a 21 m station in the "Hausgarten" at Boknis Eck estimated that up to 430 g C m^{-1} yr^{-1} is consumed, much more than 105 g C m^{-2} yr^{-1} at a 10 m station (Graf et al., 1984). The 3 different types of sediment may thus be characterized as follows:

Erosion areas:

sand with high turbulence, small OM reservoir, food supply mainly from biodeposition and benthic primary production, diurnal cycles, no deposition of OM. low heat production

High combustion areas:

muddy sand with alternatively stagnant and turbulent periods, medium OM reservoir, food supply mainly from sedimentation, biodeposition, and lateral advection, transitory deposition of OM, high heat production

Deposition areas:

mud with frequent stagnant periods, surplus of OM, food supply mainly from sedimentation and lateral advection, anoxia during late summer, final geological deposition, medium heat production

5. Is it just coincidence that Kiel Bight fits into steady state models?

So far several theses have been discussed, which demonstrate that 1) the patterns and the processes of benthic-pelagic coupling are very complicated, 2) a non steady state is created, which has biological as well as geochemical consequences, 3) carbon flow through the benthos is underestimated, and 4) lateral processes are involved. Therefore, the puzzling point is that the values for pelagic primary production and benthic oxygen consumption of Kiel Bight fit into the steady state model (cf. fig. 1).

To explain the good food supply and the corresponding high combustion values for OM by lateral advection and by biodeposition arises another question. What processes fill the OM pool of the resuspension loop? Vertical sedimentation in the range of 40 - 60 g C $m^{-2}yr^{-1}$ (Smetacek, 1980) can account for only a fraction.

In Kiel Bight the supply of macroalgae is important (Graf et al., 1983). Based on the tracer lutein, a carotinoid, which in Kiel Bight is derived from red algae, it was estimated that production by macroalgae is 10-15% of the pelagic primary production (Abele, 1988). The disrupted and drifting macroalgae are not seen in sediment traps. However, in the high combustion and the deep deposition areas macroalgae may contribute as much OM as does pelagic primary production. In addition near-bottom down slope transport of pellets produced by shallow water suspension feeders may be important. Assuming that Laf*S + BD double the vertical pelagic input of 40-60 g C m^{-2} yr^{-1} , and that macroalgae can add another 100 g C m^{-2} yr^{-1}, the mean food supply for subpycnocline sediments should be more than 200 g C m^{-2} yr^{-1}. This is in the range of the annual OM demand of 105 to 430 g C m^{-2} yr^{-1}

given above. A mean consumption rate in the subpycnocline sediments may be 200 - 300 g C $m^{-2}yr^{-1}$.

An answer to our question may be given by the findings of Grant and Hargrave (1987). They found that oxygen consumption seems to be correlated with a certain fraction of OM only and that the most labile fraction, representing only a few percent of total OM, is responsible for the correlation between oxygen consumption and available OM. To apply this hypothesis to our model we have to postulate that the labile OM fraction fills the pool of the resuspension loop via vertical sedimentation in a constant ratio to the total OM input, so that pelagic primary production and benthic oxygen consumption are indirectly correlated. If the most labile OM fraction is a constant fraction of settling OM, the correlation may even be highly significant.

High quality food is quickly consumed and will only shortly be part of the resuspension loop. Statistically, refractory material has a much higher chance to be transported into the high combustion and deposition areas. Therefore, in terms of oxygen consumption, which is closely related to the most labile OM fraction, the difference between high combustion areas and deserts in Kiel Bight is by a factor of 2 (Pollehne, 1986). This difference, however, is by a factor of 4 when measured by heat production (Graf et al., 1984). A similar result is indicated by experiments of Grant and Hargrave (1987). They reported that $CO_2:O_2$ ratio increased, when the labile OM fraction was consumed, indicating a long term shift towards anaerobic metabolism. The latter finding would also increase the ratio of heat production versus oxygen consumption.

Thus, it seems that indirect relationships are responsible for the observation that Kiel Bight apparently fits into the steady state model. It is

obvious that future research should concentrate on the lateral, near-bottom processes; this necessitates the combined effort of geological and biological disciplines. In order to advance beyond just statistical descriptions methods must be developed, which allow the direct quantification of all the above mentioned fluxes .

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